


POPULATION DYNAMICS OF TUNDRA SWANS  
ON THE LOWER ALASKA PENINSULA

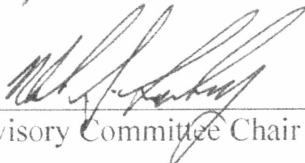
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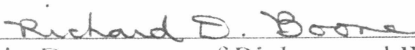
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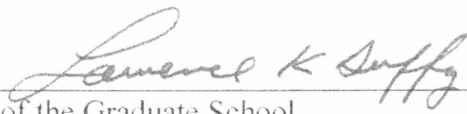
  
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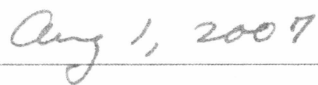
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POPULATION DYNAMICS OF TUNDRA SWANS  
ON THE LOWER ALASKA PENINSULA

A  
THESIS

Presented to the Faculty  
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements  
for the Degree of

MASTER OF SCIENCE

By

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## **ABSTRACT**

This study was initiated in response to concerns regarding apparent declines in abundance and breeding pair density of tundra swans on and adjacent to Izembek National Wildlife Refuge (NWR) on the lower Alaska Peninsula. I conducted an analysis of long-term data (1978–1996) to estimate demographic parameters and assess the relationship between survival probabilities and a number of environmental and ecological factors. Rates of productivity (egg, nest, cygnet survival) and annual rates of apparent adult survival were lower and more variable than previously observed for other swan populations and species. A negative relationship between nesting success and brown bear density indicates that depredation by bears is a primary determinant of tundra swan reproductive success. Changes in apparent survival probability were primarily influenced by high and variable rates of permanent emigration. Because of low rates of production and apparent survival, immigration by swans from other breeding areas may be important for sustaining a breeding population of tundra swans on and adjacent to Izembek NWR.

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## GENERAL INTRODUCTION

The number of individuals in any given natural population is inherently variable through time and space as a result of reciprocation between the positive (birth, immigration) and negative (death, emigration) population processes (Gotelli 1988). Although knowledge of variation in abundance is of considerable importance for identifying trends in population status, this information alone does not provide insight into why changes in population status occur, nor which demographic parameters are the most important determinants of population change (Johnson et al. 1992). Therefore, effective management decisions require knowledge of demographic parameters and variation in those parameters as related to intrinsic and extrinsic factors (Mills and Lindberg 2002).

The primary impetus of wildlife management is to sustain population abundance at desired levels and maintain biodiversity by preventing population and species extinction. The influence of environmental and demographic stochasticity on population dynamics is negatively correlated with population size, such that small populations are more prone and sensitive to fluctuations in abundance; and ultimately, their risk of extinction is greater than that of large populations (Lande et al. 2003). Furthermore, stochastic variation in demographic parameters alone, even without changes in mean values, is expected to result in reduced long-term population growth rates (Tuljapurkar 1982). Therefore, the need for detailed population data is particularly pressing for small populations that are declining, may be exposed to changes in habitat conditions, or are



subject to potential changes in harvest. In response to proposals for increased development and harvest pressure, and an apparent 75% reduction in nesting pair density between 1980 and 2003, we initiated a retrospective demographic assessment of tundra swans (*Cygnus columbianus columbianus*) on and adjacent to Izembek National Wildlife Refuge (NWR) on the lower Alaska Peninsula.

Tundra swans breed in coastal lowlands of Alaska and Canada from the Arctic Coastal Plain to the Aleutian Islands (Limpert et al. 1991). Tundra swans of the lower Alaska Peninsula breed at the southern extremity of the species breeding range and exhibit unique non-migratory behavior (Dau and Sarvis 2002). Unlike their counterparts in more northern latitudes, tundra swans associated with areas on and adjacent to Izembek NWR (hereafter: Izembek population) are known to winter in Alaska and have been observed in large concentrations during winter months on Unimak Island near their breeding grounds (Dau and Sarvis 2002). Annual spring census data indicate that population abundance fluctuated considerably among years (range: 57–266; Chapter 2, Fig. 3), and Dau and Sarvis (2002) suggested that large reductions in abundance were a result of large-scale emigration events. During 1977–2006, Izembek NWR biologists conducted studies of the Izembek population. In addition to surveys documenting the abundance of pairs and nests, a total of nearly 500 active nests were monitored during the nesting season. Additionally, successfully hatched cygnets from those nests were monitored regularly to determine their fate, and more than 700 swans were captured and marked with neckbands (Dau and Sarvis 2002). Observations of marked swans were recorded during subsequent summers and during the winter on Unimak Island. I

analyzed these data using state-of-the-art techniques to examine life history parameters of survival and productivity and thereby gain knowledge of the factors influencing the observed variation in abundance of the population.

My primary objectives were to estimate individual population parameters and assess the effects of environmental and ecological factors on variation in these parameters. Previous studies of breeding tundra swans in Alaska indicate that productivity increases with distance south of the Arctic, primarily as a result of longer breeding seasons in southern latitudes (Wilk 1988, Monda et al. 1994, Babcock et al. 2002). However, Dau and Sarvis (2002) reported apparent estimates of egg and cygnet survival for the Izembek breeding grounds that were considerably lower than those reported in northern breeding locations. Therefore, I was interested in identifying the factors that influenced reproductive success on the Izembek breeding grounds and assessing the degree to which those factors may have differed from other breeding areas (Chapter 1). Specifically, I sought to describe variation in daily survival probabilities of eggs, nests, and cygnets relative to predator densities, daily fluctuations in weather (temperature and precipitation), timing of the breeding season, and age of cygnets. Life history theory predicts that long-lived waterfowl species such as swans and geese should exhibit relatively high and stable rates of adult survival, and that adult survival is usually the most influential parameter on population growth rates (Lebreton and Clobert 1991). Because population abundance declined between 1980 and 2003, I was interested in estimating annual survival probabilities of post-fledging swans to assess the degree of variation in this parameter (Chapter 2). Furthermore, I sought to describe variation in

rates of apparent survival relative to age and sex class. Finally, because estimates of demographic parameters contingent on a sample of marked individuals are subject to bias associated with marker loss (Arnason and Mills 1981, Nichols and Hines 1993), I sought to estimate annual rates of collar loss and assess variation in rates of loss among age and sex classes.

## CHAPTER 1

### PRODUCTIVITY OF TUNDRA SWANS BREEDING ON THE LOWER ALASKA PENINSULA<sup>1</sup>

**Abstract:** The number of breeding tundra swan pairs on and adjacent to Izembek National Wildlife Refuge on the lower Alaska Peninsula fluctuated considerably (range: 23–86) between 1980 and 2006. We investigated patterns in tundra swan productivity to gain insight into the ecological processes acting on the population and identify management priorities. We monitored tundra swan nests and broods via aerial surveys (1980–96) and applied plastic neckbands to pre-fledged cygnets. Because methods of data collection varied over time, we conducted 2 separate analyses to estimate nest, egg, and cygnet survival rates during 1980–87 and a third, less detailed analysis, to assess long-term variation in productivity during 1980–96. Additionally, we estimated mean apparent nest survival rates to allow direct comparison of our estimates to those in other breeding areas of Alaska. Daily survival probabilities of nests varied annually, decreased as the breeding season progressed, and varied between those nests located along the road system and those in remote areas of the refuge. Nest survival probabilities were higher and less variable in proximity to the city of Cold Bay (mean = 0.77, range: 0.63–0.91) as

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<sup>1</sup> Prepared for submission to *The Journal of Wildlife Management* as Meixell, B. W., M. S. Lindberg, C. P. Dau, J. E. Sarvis, and K. M. Sowl. Productivity of tundra swans breeding on the lower Alaska Peninsula.

compared to remote areas (mean = 0.38, range: 0.18–0.71), where brown bear density was considerably higher. Cygnet survival probability to fledging varied by year (mean = 0.55, range: 0.31–0.83), increased with cygnet age, and decreased by an average of 0.03 following neckbanding. Combining nest success, cygnet survival, and egg survival, (1980–87) yielded yearly estimates of the probability that an egg produced a fledged cygnet ranging from 0.03 to 0.44. Estimates of the probability that a nest produced a fledged cygnet indicate that productivity in remote areas was stable over time (1980–87: 0.10, 1988–96: 0.11), while productivity near the city of Cold Bay declined (1980–87: 0.46, 1988–96: 0.03). Our estimates of nest survival in remote areas were lower than those reported elsewhere in Alaska, and negative relationships between nesting success and bear density suggest that depredation by bears is a primary determinant of reproductive success. We recommend that the goals and objectives of bear management take into consideration the likely effects of bear density on tundra swan productivity.

**Key words:** Alaska, Alaska Peninsula, brown bear, cygnet survival, *Cygnus columbianus*, nest survival, population dynamics, productivity, tundra swan, *Ursus arctos*

## INTRODUCTION

Effective management decisions require knowledge of population dynamics and should consider the relative influence of demographic parameters on population growth as well as the vital rates that managers have the ability to change (Caswell 2000, Wisdom

et al. 2000). Reproduction is an integral component of waterfowl population dynamics (Johnson et al. 1992) and is the primary source from which new individuals enter a population. In long-lived waterfowl species (i.e., swans and geese), low rates of productivity are balanced by high survival rates (Charlesworth 1994), and adult survival usually has the greatest influence on population growth (Lebreton and Clobert 1991). However, productivity may have considerable effects on population growth in wild populations if the annual variation in productivity exceeds that of other, more influential, demographic parameters (Schmutz et al. 1997, Cooch et al. 2001, Flint et al. 2006). Therefore, knowledge of the underlying processes affecting productivity is important for identifying factors influencing variation in population abundance and establishing management priorities.

Tundra swans (*Cygnus columbianus columbianus*) breed in coastal lowlands of Alaska and Canada from the Arctic Coastal Plain to the Aleutian Islands (Limpert et al. 1991) and exhibit substantial spatial variation in reproductive success. Arctic breeding swans nest at lower densities, lay smaller clutches, and produce fewer cygnets than those nesting to the south on the Yukon-Kuskokwim (Y-K) Delta and Bristol Bay lowlands (Wilk 1988, Monda et al. 1994, Babcock et al. 2002). On the Y-K Delta and Arctic Coastal Plain, late springs were directly correlated with reduced productivity, while in southern latitudes near Bristol Bay, late springs did not affect productivity (Lensink 1973, Wilk 1988, Ritchie et al. 2002). Tundra swans breeding in the Bristol Bay lowlands produced the largest number of cygnets and experienced the least amount of annual variation in productivity (Wilk 1988), while reproductive success of Arctic-

nesting swans varied considerably among years (Monda et al. 1994, Ritchie et al. 2002). Lower productivity in the Arctic was likely a result of weather conditions limiting the length of the breeding season (King 1970, Babcock et al. 2002), and therefore swans nesting in areas with longer breeding seasons may have more stable populations (Wilk 1988). The threat of predation to tundra swan nests is typically low as a result of the large size and aggressive behavior of adults (Hawkins 1986), although in some tundra swan breeding areas, brown bears (*Ursus arctos*, hereafter: bears) pose a threat to tundra swan reproductive success (Monda et al. 1994).

Tundra swans on and adjacent to Izembek National Wildlife Refuge (NWR) on the Lower Alaska Peninsula (hereafter: Izembek population) represent the most southwesterly breeding population. The Izembek population is the only known population of tundra swans to exhibit non-migratory behavior, and in most winters between 1978–1996, the majority of birds wintered on the breeding grounds or on nearby Unimak Island (Dau and Sarvis 2002). However, during the winters of 1987–89, a large proportion of the population migrated out of Alaska to the Pacific Northwest (Dau and Sarvis 2002). Densities of breeding pairs and the number of nest attempts immediately following migration events were significantly reduced (Dau and Sarvis 2002). Additionally, breeding pair densities declined by nearly 75% between 1980 and 2003 (Dau and Sarvis 2002, Izembek National Wildlife Refuge, unpublished data). As part of an ongoing study to identify factors affecting the population growth rate of the Izembek population, we analyzed 17 years of productivity data to: 1) estimate survival probabilities of nests, eggs, and cygnets, 2) assess the effects of weather, bear densities,

cygnet age, season date, and neckbanding on survival, 3) compare productivity of southern-nesting swans to those in higher latitudes, and 4) provide recommendations for management of swans breeding on the lower Alaska Peninsula.

## STUDY AREA

We monitored tundra swan nests and broods on a 1,071-km<sup>2</sup> area on and adjacent to Izembek National Wildlife Refuge (55°10'N, 162°40'W) on the western end of the Alaska Peninsula (Fig. 1). Approximately 95% of the refuge was designated as wilderness and is bordered by the Bering Sea to the northwest and Pacific Ocean to the southeast. Characteristics of the landscape included volcanic mountains, glaciers, valleys, coastal lagoons, wetland complexes, and ericaceous uplands with interspersed lakes. Breeding tundra swans used two distinct types of wetland complexes: 1) shallow closed-basin oligotrophic lakes, and 2) shallow open-basin eutrophic lakes with abundant aquatic vegetation (e.g., pond weeds [*Potamogeton spp.*] and water milfoil [*Myriophyllum spp.*]) and turbid water (Dau and Sarvis 2002). The area supports an abundance of summer and fall salmon runs and high brown bear densities (Miller et al. 1997). The lower Alaska Peninsula is influenced by the Aleutian maritime climate, which results in earlier thaws and later freezes than in the arctic and subarctic, allowing for comparatively longer breeding seasons. Weather conditions during the breeding season (April–August) were cool (mean daily temperature = 7.0 °C), windy (mean wind



speed =  $27.0 \text{ km} \cdot \text{h}^{-1}$ ), wet (mean monthly precipitation = 7.0 cm), and cloudy (mean number of overcast days per month = 27.4).

Bear density on the Cold Bay road system (road system), a  $200\text{-km}^2$  portion of our study area surrounding the city of Cold Bay (Fig. 1), varied considerably over time as a result of changes in harvest regulations. Following the closure of bear hunting on the road system in 1969, bear density increased to levels that led to safety concerns by the residents. In response, a liberal hunting season was initiated in 1975. Forty-five bears were harvested in the subsequent 30 months, reducing bear density to an estimated 1-bear/ $40 \text{ km}^2$  in 1982. In contrast, bear density in the remaining portion of our study area ( $871 \text{ km}^2$ ) was believed to be stable over time with 1982 bear density estimates of 1-bear/ $12 \text{ km}^2$ . Therefore, during the early part of our research (1980–87) bear density was likely lower on the road system than in remote areas. However, following harvest restrictions in 1984, bear density on the road system increased, although the rate and extent of the increase was not documented (Dau 1989).

## **METHODS**

### **Data Collection**

We observed nests and broods via aerial surveys from a Piper PA-18 aircraft and from the ground where possible (<2% of observations). We conducted surveys annually from 1980–96 beginning in late April or early May and continuing through mid- to late August. Survey days were opportunistic due to frequent adverse weather conditions on

our study area. Nest and brood revisit intervals usually ranged from 3 to 7 days during 1980–87 and from 2 to 4 weeks during 1988–96. We surveyed all available tundra swan habitat on the study area and recorded nest and brood locations on 1:63,360 topographic maps. When weather conditions permitted, we could survey the entire study area in approximately 5.5 flight hours. During each survey, we revisited all previously located nests and surveyed the entire study area for newly initiated nests. During nest revisits, we attempted to record clutch size by hazing the incubating adult from the nest. To minimize disturbance and ensure accurate clutch size counts, we only performed clutch counts when we were confident that the female had completed egg laying and limited clutch count attempts to 1–3 times per season for a given nest. We recorded brood sizes on all revisits as cygnets could be observed from higher altitudes and, thus, required little disturbance.

We captured a subset of family groups with dip nets from a taxiing floatplane, small boats, or by hand beginning in late July (1980–88, 1990–95) when cygnets were nearing flight stage. We marked adults and cygnets with plastic neck and tarsus bands with engraved alphanumeric characters and U.S. Fish and Wildlife Service metal tarsus bands. We released parents and their offspring together after banding.

### **Data Analysis**

We used Program MARK (White and Burnham 1999) to obtain maximum likelihood (ML) estimates of daily survival probability (DSP) of nests, eggs, and cygnets and to assess the effect of a number of covariates on tundra swan productivity. This method is an extension of the model developed by Johnson (1979) and Bart and Robson

(1982) that uses generalized linear models (McCullough and Nelder 1989) to examine the relationships between DSP and independent variables of interest (covariates; Dinsmore et al. 2002).

Because the interval length of nest and brood revisits changed considerably during our study, we split our analyses and applied more detailed models to years with more frequent visitation. We applied detailed analytical techniques to the productivity data for 1980–87 in two analyses: 1) nest survival and 2) egg and cygnet survival. To assess long-term variation in productivity we conducted a third, general analysis, on data collected during 1980–96, in which we estimated DSP of nests and broods without distinguishing between life stages.

We used an information theoretic approach (Burnham and Anderson 2002) to assess support for a number of competing hypotheses about tundra swan productivity on our study site. To limit the total number of models, we performed model selection using a 2-stage hierarchical approach. In the first stage, we began each of 3 analyses with a set of candidate models that described competing hypotheses about variation in productivity through time (hereafter: temporal models). We assessed temporal variation among years by fitting models as constant ( $\cdot$ ), year-specific (year), and linear (YEAR) and quadratic (YEAR<sup>2</sup>) trends. We assessed temporal variation within-year (season) by fitting models as constant ( $\cdot$ ) and as linear (T) and quadratic (T<sup>2</sup>) time trends. Time trends were fitted as additive (1 slope applied to all years) and interactive (year-specific; unique slope applied to each year). We expected DSP to vary among and within years as a result of potential

changes in seasonal weather patterns, daily weather events, predator density, and predator behavior.

In the second stage of the hierarchy, we selected the best approximating temporal models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002) and constructed additional models by adding more detailed and biologically relevant covariates (hereafter "specific covariates"). We advanced a subset of models ( $\Delta\text{AICc} < 4$ ), as opposed to just the top model, from the first hierarchical stage to account for model selection uncertainty and because less parameterized models may perform better when fitted with additional parameters. Due to the complex model structure in the egg and cygnet survival analysis, we increased the temporal-model cutoff point to 8  $\Delta\text{AICc}$  to allow less parameterized models to be advanced to the second stage. We used weather data collected at the Cold Bay airport and assessed the effects of minimum daily temperature (temp) and daily precipitation (precip). Inclement weather has been identified as a primary factor affecting overall gosling production (Schmutz et al. 2001, Johnson and Noel 2005), and studies of incubating geese and swans indicate that incubation constancy and behavior are influenced by daily weather patterns (e.g., Eichholz and Sedinger 1999). Furthermore, studies of nesting geese suggest a correlation between nest attentiveness and egg predation (Afton and Paulus 1992). We hypothesized that DSP of nests and eggs would be related to daily fluctuations in temperature and precipitation and that cygnet DSP would decrease during periods of adverse weather.

We selected the most parsimonious models from each analysis ( $\Delta\text{AICc} < 4$ ) to create a subset of models for inference. We model-averaged coefficient (beta) estimates from each subset, after re-weighting  $w_i$ , to reduce bias, account for model selection uncertainty, and avoid overestimating precision (Burnham and Anderson 2002). We calculated the relative importance of predictor variables  $x_j$  as the sum of  $w_i$  across all models in the set where variable  $j$  occurred ( $w_+(j)$ ; Burnham and Anderson 2002). We back-transformed estimates of DSP from the logit link and produced survival probability estimates as the product of all DSP over the appropriate incubation (31 days) or brood rearing (65 days) period (referred to as DSP derived estimates; Limpert and Earnst 1994). We present year-specific survival probabilities representative of the mean nest where Day 1 corresponds to the mean day of incubation onset, 15 May (14 May in leap years). We used the delta method (Seber 1982) to calculate variances associated with back-transformed survival estimates and model-averaged predicted survival estimates because not all parameters were directly comparable (Burnham and Anderson 2002).

*Nest Survival (1980–87).* Brown bears were suspected to be an important predator of tundra swan nests on our study area, and estimates of brown bear density in 1982 were approximately 3 times lower on the 200-km<sup>2</sup> road system than in adjacent, more remote, areas (871 km<sup>2</sup>) off of the road system (Dau 1989). Therefore, we assessed variation in DSP between the 2 locations and expected survival to be higher on the road system than in remote areas as a result of differences in bear densities. We investigated an additional within-season variable by partitioning the nesting season into 6, 2-week intervals to assess a higher degree of within-season variation than was possible with

linear and quadratic trend variables. We relied on sightings of cygnets to determine nest fate and, when necessary, estimated hatch date based on cygnet size. Long revisit intervals over the hatching period made it difficult to distinguish between unsuccessful nests and successful nests that suffered entire brood loss. Therefore, when revisit intervals were longer than 12 days, we right-censored data for all encounter histories back to the previous date of known fate.

Estimates of tundra swan nest survival in the literature are limited to estimates of apparent nest survival, which may be positively biased because short-lived nests are under-represented in the sample (Mayfield 1961). To allow direct comparison of our results to those elsewhere in Alaska, we calculated mean apparent nest success (AS; number of successful nests/number of total nests) for the entire study area and separately for nests on the road system and in remote areas for 1980–87.

*Egg and Cygnet Survival (1980–87).* We simultaneously modeled DSP of eggs and cygnets from nests that successfully hatched at least one cygnet (successful nests). Egg survival was the probability that an egg from a successful nest hatched (31 days), cygnet survival was the probability that a hatched cygnet survived to flight stage (65 days), and breeding-season productivity was the probability that an egg from a successful nest produced a fledged cygnet (96 days). We assessed the effect of cygnet age (cygage) and plastic neckbands (collar) on cygnet survival and predicted that cygnet DSP would increase with age and decrease following capture and neckbanding. Due to data limitations, we did not assess annual variation in egg survival.

Our data differed from traditional ground-based waterfowl productivity data, because we were unable to count the number of successfully hatched membranes from the aircraft. This caused a level of uncertainty; if we observed more eggs in a nest prior to hatch than cygnets in the first revisit post-hatch, it is unknown whether the discrepancy occurred due to 1) eggs that were depredated prior to hatch, 2) eggs that were nonviable or did not hatch, or 3) eggs that successfully hatched and died as cygnets prior to the first revisit post-hatch. Therefore, we used the observer effects model (Rotella et al. 2004) to estimate a transitional mortality event (TME) that occurred during the transition from egg to cygnet as an intercept adjustment that included all sources of mortality to eggs or cygnets over the interval between the last visit pre-hatch and first visit post-hatch (hatching interval). Each model of survival ( $\hat{S}$ ) contained 3 components; 1) egg survival, 2) hatching interval survival (TME), and 3) cygnet survival:

$$\hat{S} = \left[ \left( \hat{\beta}_{\text{egg}_0} + \hat{\beta}_{\text{egg}_1} * X_{\text{egg}_1} \dots \hat{\beta}_{\text{egg}_i} * X_{\text{egg}_i} \right) * \left( \hat{\beta}_{\text{TME}} \right) * \left( \hat{\beta}_{\text{cyg}_0} + \hat{\beta}_{\text{cyg}_1} * X_{\text{cyg}_1} \dots \hat{\beta}_{\text{cyg}_i} * X_{\text{cyg}_i} \right) \right]$$

where, the  $\hat{\beta}_{\text{egg}_i}$ ,  $\hat{\beta}_{\text{TME}}$ , and  $\hat{\beta}_{\text{cyg}_i}$  are the respective estimated regression coefficients for egg survival, TME, and cygnet survival, and  $X_{\text{egg}_i}$  and  $X_{\text{cyg}_i}$  are the values of the independent variables for egg survival and cygnet survival, respectively.

The first day of observation was the date of first clutch count, and nests without clutch counts were omitted from the egg survival and TME components. Cygnets were assumed to have fledged if they were observed alive on or after their calculated fledge date (65 days post hatch). If cygnet observations were not performed on or after their calculated fledge date, or the breeding pair could not be located, data were right-censored back to the last date cygnets were observed alive.

*Overall Productivity (1980–87).* We define overall productivity as the probability that an egg successfully produces a fledged cygnet. We estimated overall productivity for the years 1980–87 as the product of model averaged nest survival, egg survival, TME, and cygnet survival, using year-specific and mean covariate values.

*Long-term Productivity (1980–96).* We assessed long-term variation in tundra swan productivity, 1980–96, by estimating DSP of nests and broods without differentiating between life stages (nests and broods), utilizing the less detailed data collected after 1987. Survival over the breeding season was the probability that at least 1 cygnet from a nest reached flight stage, over 96 days to account for incubation and brood rearing periods. Because hatch dates could not be determined for all nests, broods were considered to have fledged if at least one cygnet was observed alive on or after 25 August.

Because migratory behavior of swans and bear densities varied among the periods of 1980–87 and 1988–1996, we considered additional sources of variation in productivity not included in our previous analyses. In the years immediately following the unusual migration events during the winters of 1987–89, the number of initiated nests and breeding pairs were significantly reduced (Dau and Sarvis 2002). To assess the effect of the migration events on productivity, we modeled DSP in two groups: pre- (premig, 1980–87) and post- (postmig, 1988–1996) migration. Furthermore, bear densities on the road system are believed to have increased in the late 1980s as a result of restrictive harvest regulations implemented in 1984 (Dau 1989). Therefore, in addition to a constant road system effect, we assessed differences in the road system effect before



(preroad, 1980–87) and after (postroad, 1988–96) migration events. Due to long revisit intervals, our data likely did not have the resolution to precisely estimate daily weather effects. As an alternative, we assessed the effect of annual weather indices. We constructed a storm index (sdprecip) by calculating the standard deviation of the mean precipitation in each year, where a larger standard deviation represented years with larger rain events. We expected storm events to negatively affect productivity and therefore hypothesized that reproductive success would be lower in years with high sdprecip. We calculated a temperature index (mintemp) by summing the number of days during the breeding season for which the daily minimum temperature was 2 °C or less. This was a below average temperature that could potentially alter incubation behavior and challenge the thermoregulatory ability of cygnets.

## RESULTS

### Nest Survival (1980–87)

We analyzed encounter histories of 262 tundra swan nests with a total of 4,889 exposure days. Of all nests, 53.1% survived and 45.8% failed, (1.1% were right-censored due to long revisit intervals). Mean apparent nest success was 0.79 for nests on the road system (SE = 0.04, range: 0.67–1.0,  $n = 67$ ), and 0.48 for nests in remote areas (SE = 0.06, range: 0.24–0.82,  $n = 192$ ).

We assessed variation in DSP of tundra swan nests by considering 25 temporal models and an additional 23 specific-covariate models; we present estimates from the top

11 approximating models ( $\sum w_i = 0.99$ ; Table 1). DSP was higher on the road system than in remote areas ( $\hat{\beta}_{\text{road}} = -1.363$ ,  $\hat{SE} = 0.296$ ), increased with warmer daily minimum temperatures ( $\hat{\beta}_{\text{temp}} = 0.013$ ,  $\hat{SE} = 0.024$ ), and decreased with increasing levels of daily precipitation ( $\hat{\beta}_{\text{precip}} = -0.176$ ,  $\hat{SE} = 0.006$ ). We found support for additive ( $\omega_+ (j) = 0.46$ ) and year-specific ( $\omega_+ (j) = 0.40$ ) within-season trends in DSP; logit-linear trends were negative in models with an additive trend ( $\hat{\beta}_T = -0.018$  to  $-0.023$ ,  $\hat{SE} = 0.008, 0.012$ ) and in all years for models with year-specific trends ( $\hat{\beta}_{T*year} = -0.119$  to  $-0.018$ ,  $\hat{SE} = 0.052, 0.020$ ), except 1981 ( $\hat{\beta}_{T1981} = 0.008$  to  $0.021$ ,  $\hat{SE} = 0.019, 0.017$ ). Among all covariates, road received the greatest support ( $\omega_+ (j) = 1.0$ ), and the additional variables T ( $\omega_+ (j) = 0.86$ ), precip ( $\omega_+ (j) = 0.44$ ), and temp ( $\omega_+ (j) = 0.39$ ) were also supported (Table 1). Average nest survival was 0.77 (95% CI = 0.71, 0.82) on the road system and 0.38 (95% CI = 0.30, 0.46) in remote areas. Nest survival probability was lowest in 1981, (road system: 0.63, 95% CI = 0.41, 0.85; remote: 0.18, 95% CI: 0.00, 0.37) and highest in 1984, (road system: 0.91, 95% CI = 0.70, 1.00; remote: 0.71, 95% CI: 0.38, 1.00; Table 2).

### **Egg and Cygnet Survival (1980–87)**

We analyzed encounter histories of 703 eggs and cygnets from 149 successful nests for a total of 30,248 exposure days. Of 485 eggs, 74.0% produced cygnets and 22.1% died in an unknown life stage. Of 587 cygnets, 34.7% were known to have fledged and 23.9% were right-censored, because the last observations occurred prior to the calculated fledge date.

We considered 16 temporal models and an additional 62 specific-covariate models to assess variation in DSP of tundra swan eggs and cygnets; we present model-averaged estimates from the top 3 approximating models ( $\sum w_i = 0.997$ ; Table 3). DSP of eggs decreased with warmer daily minimum temperatures ( $\hat{\beta}_{\text{eggtemp}} = -0.278$ ,  $\hat{SE} = 0.110$ ) and increasing levels of daily precipitation ( $\hat{\beta}_{\text{eggprecip}} = -0.989$ ,  $\hat{SE} = 0.222$ ). DSP of cygnets increased with cygnet age (range:  $\hat{\beta}_{\text{cygage}} = 0.062$  to  $0.126$ ,  $\hat{SE} = 0.012, 0.035$ ), but decreased with warmer daily minimum temperatures ( $\hat{\beta}_{\text{cygtemp}} = -0.156$ ,  $\hat{SE} = 0.049$ ) and following neckbanding ( $\hat{\beta}_{\text{collar}} = -2.427$ ,  $\hat{SE} = 0.521$ ).

DSP for an egg in a successful nest was 0.995 ( $\hat{SE} = 0.001$ ) with mean weather values and ranged from 0.602 ( $\hat{SE} = 0.093$ ; high temp, high precip) to 0.999 ( $\hat{SE} = 0.017$ ; low temp, low precip). Average cygnet DSP was lowest the day after hatch (mean = 0.962,  $\hat{SE} = 0.019$ ) and highest at 65 days post hatch (mean = 0.9996,  $\hat{SE} = 0.0002$ ). The application of a neckband at the mean age of banding (55 days) reduced the probability that a cygnet would survive to fledging by an average of 0.031 (range: 0.020–0.034). Cygnet survival for non-neckbanded cygnets was lowest in 1980, 0.31 (95% CI = 0.17, 0.45), and highest in 1987, 0.83 (95% CI = 0.73, 0.94). In the absence of total nest failure, the probability that an egg survived to flight stage ranged from 0.15 (95% CI: 0.08, 0.22) in 1981 to 0.50 (95% CI: 0.40, 0.60) in 1984. On average, egg survival was 0.69 (95% CI: 0.65, 0.73), survival over the hatching interval (TME) was 0.86 (95% CI: 0.64, 1.00), and cygnet survival was 0.55 (95% CI: 0.51, 0.60; Fig 2).

## Overall Productivity

We determined overall productivity rates (1980–87), the probability that an egg produces a fledged cygnet, by taking the product of model-averaged nest survival, egg survival, cygnet survival and TME probabilities. Average productivity was higher on the road system (0.26, 95% CI: 0.20, 0.33) than in remote areas (0.14, 95% CI: 0.05, 0.23). Productivity on the road system was lowest in 1982 (0.12, 95% CI = 0.00, 0.29) and highest in 1984 (0.46, 95% CI = 0.33, 0.59), while in remote areas it was lowest in 1981 (0.03, 95% CI = 0.00, 0.22) and highest in 1984 (0.38, 95% CI = 0.10, 0.65).

## Long-term Productivity (1980–96)

We analyzed encounter histories from 471 nests and broods for a total of 20,188 exposure days. We assessed variation in DSP of tundra swan nests and broods by considering 14 temporal models and an additional 39 specific-covariate models; only 4 models received reasonable levels of support ( $\sum w_i = 0.999$ , Table 4).

DSP was higher pre-migration ( $\hat{\beta}_{premig} = 3.93$ ,  $\hat{SE} = 0.37$ ) than post-migration (1988–1996;  $\hat{\beta}_{postmig} = 2.36$ ,  $\hat{SE} = 0.41$ ). DSP was higher on the road system during 1980–87 ( $\hat{\beta}_{preroad} = -1.12$ ,  $\hat{SE} = 0.21$ ), but higher in remote areas during 1988–1996 ( $\hat{\beta}_{postroad} = 0.51$ ,  $\hat{SE} = 0.26$ ). DSP increased as the breeding season progressed ( $\hat{\beta}_T = 0.020$ ,  $\hat{SE} = .003$ ), was lower during years with large precipitation events ( $\hat{\beta}_{sdprecip} = -0.653$ ,  $\hat{SE} = 0.053$ ), and was higher during years with warmer temperatures ( $\hat{\beta}_{mintemp} = 0.004$ ,  $\hat{SE} = 0.006$ ).

Average survival over the breeding season, the probability that at least one cygnet from a nest reached flight stage, was highest on the road system pre-migration, 0.46

(95% CI: 0.33, 0.60) and lowest post-migration, 0.03 (95% CI: 0.00, 0.07). Productivity in remote areas was similar pre- (0.10, 95% CI: 0.06, 0.14) and post- (0.11, 95% CI: 0.06, 0.16) migration.

## **DISCUSSION**

### **Modeling Productivity**

The estimation of survival probability from our model requires that: 1) ages are determined accurately, 2) fates are determined with known certainty, 3) fates are not influenced by observers, 4) fates are independent, and 5) daily survival probabilities are homogeneous (Dinsmore et al. 2002). Cygnet ages were determined by backdating to hatch date, and hatch dates were generally known plus or minus 2 days. Nests with unknown fates (all analyses) or re-visit intervals longer than 12 days (nest, egg and cygnet survival analysis) were right-censored back to the last date of known fate. Right-censoring of survival data should not cause bias if the samples were random (i.e., nests with long revisit intervals were not more likely to hatch or fail than the population as a whole; Bunck et al. 1995). Most nest and brood visits were conducted from aircraft (>98%), so disturbance to nests was minimal, although incubating adults were disturbed when we flew at low altitudes to conduct clutch counts. Swan nests are generally not clustered, although some positive spatial correlation (dependence) among nests may have existed. Bears occupy a relatively large home range and therefore may be more likely to destroy nests in close proximity to one another. Nest site selection may reduce the

vulnerability of some nests to predation, and some pairs may have been better at successfully producing hatchlings and fledglings due to age and experience. However, incubating swans are highly visible and nesting habitat throughout our study area was generally homogeneous, so we suspect that detection of nests by bears was for the most part unrelated to nesting sites. Furthermore, once a bear detects a nest, we suspect that the probability of predation is nearly 100%, regardless of nest location or previous breeding experience. Therefore, all of our data probably met the first three assumptions, and our nest survival data probably met all assumptions. However, we suspect that assumptions 4 and 5 were violated to some degree in our analysis of egg and cygnet survival. Some dependence among eggs in a nest and among brood mates probably existed. Therefore, we may overestimate precision associated with egg and cygnet survival to an unknown degree (Williams et al. 2002).

### **Effects of Bears on Productivity**

Tundra swans are large birds that defend their nests aggressively and are capable of deterring most nest predators, with the exception of bears (Babcock et al. 2002). Brown bears are responsible for considerable declines in nest survival of tundra swans and lesser snow geese on the Arctic slope of Alaska (Monda et al. 1994, Johnson and Noel 2005), and nest predation by brown bears is thought to be a significant factor in causing the population decline of dusky Canada geese (*Branta canadensis occidentalis*) nesting on the Copper River Delta, Alaska (Campbell 1990). Brown bear densities on the lower Alaska Peninsula are among the highest for tundra swan breeding locations in Alaska (Miller et al. 1997), and we suspect that the majority of nest failures are a result

of depredation by bears. Dau (1989) reported that bear densities were considerably lower on than off of the road system during 1980–88, and estimates from 1982 indicated that bear densities were more than 3 times higher in adjacent remote areas off of the road system. We found overwhelming support for differential nest survival between bear management areas, where survival probabilities averaged 0.027 higher per day for nests on the road system. Nest survival probability was higher on the road system in all years and 8-year average survival was 0.44 higher. As a result, our estimates of overall productivity indicated that on average, an egg was more than twice as likely to produce a fledged cygnet on the road system. Additionally, while the road system accounted for only 18% of our study area (1980–87), 25% of all nests and 33% of all successful nests were located there. Given that habitat conditions and risks of nest failure excluding depredation by bears (weather patterns, abundance of non-bear predators, etc.) are similar on the road system and in remote areas, our data suggest that at high densities, brown bears can impose a substantial impact on tundra swan productivity.

Preceding studies of breeding tundra swans in Alaska indicate that productivity is lower and more variable in the Arctic where reproductive success is more sensitive to variations in weather and breeding seasons are shorter (Wilk 1988, Ritchie et al. 2002). Mean apparent nest survival rates were 0.76 (range: 0.58–0.84) on the Arctic National Wildlife Refuge (Monda et al. 1994) and 0.83 (range: 0.64–1.0) on the Central Arctic Coastal Plain (Ritchie et al. 2002). The mean apparent nest survival rate on the Y-K Delta (mean = 0.89, range: 0.73–1.0) in the sub-arctic was higher and less variable (Babcock et al. 2002). Contrary to these patterns, our estimates indicated considerable

spatio-temporal variation in productivity. Our DSP derived nest survival estimates (mean = 0.38, range: 0.18–0.71), as well as our AS estimates (mean = 0.48, range: 0.24–0.82) in remote areas were considerably lower and more variable than estimates generated elsewhere in Alaska. However, our DSP derived (mean = 0.77, range: 0.63–0.91) and AS (mean = 0.79, range: 0.67–1.00) estimates for nests on the road system were similar to other breeding areas. Because reproductive success in low bear density areas was similar to that observed elsewhere in Alaska, we suggest that our study area is capable of sustaining high rates of productivity, but that predation by bears in remote areas negated the potential positive effects associated with long breeding seasons.

DSP of nests decreased linearly as the season progressed. We were unable to account for nest age or initiation date in our models; therefore both variables are confounded with our season date parameter. Waterfowl nest success may be related to initiation date as a result of effects associated with the female (i.e., age, experience, body condition) as well as seasonal variation in predator abundance and behavior. Additionally, DSP of waterfowl nests is frequently positively correlated with nest age because nests most vulnerable to predation are destroyed early on, so that only those nests with high survival probabilities remain late in the season (Klett and Johnson 1982). However, we suspect that predation by bears may have been of sufficient magnitude to negate this inherent positive relationship, and in fact cause it to be negative. Similarly, Grand et al. (2006) speculated that a decline in DSP of Canada goose nests late in the nesting season was a result of increased predation by brown bears. Coastal brown bears forage primarily on Pacific salmon during the summer and fall, but are limited mainly to



vegetation and winter-kills (i.e., caribou, marine mammals, etc.) in the spring (Schwartz et al. 2003). As a result, bear home ranges and movements are greatest during the month of June as they travel considerable distances in search of food (Glenn and Miller 1980, C. P. Dau USFWFS, unpublished report, Schwartz et al. 2003). Average den emergence of brown bears in southern Alaska occurs in the first or second week of May (Schwartz et al. 2003), and by 25 May on the Alaska Peninsula, most bears have descended to lower elevations away from den sites (Glenn and Miller 1980). The earliest nesting swans on our study area began incubation in late April, while late-nesting swans did not initiate incubation until late May and early June. Given an incubation period of 31 days, early-initiated nests would have hatched by early May before the peak of bear activity. However, late-initiated nests would have been active through the month of June when bear abundance and movements were greatest. Therefore, we suggest that early-initiated nests were more likely to survive because they were incubated during periods of low bear activity; and regardless of age, nests were more likely to fail as the season progressed as a result of increased bear abundance and movement.

### **Effects of Weather on Productivity**

Our results indicate that annual rates of tundra swan productivity on our study area were reduced during cold and wet years primarily as a result of reduced hatching success. DSP of nests and eggs decreased as daily levels of precipitation increased, while colder daily minimum temperatures were associated with reduced nest DSP but increased egg and cygnet DSP. We expected variation in DSP associated with fluctuations in weather to result from variation in rates of nest attendance by adult swans.

Several studies identified relationships between incubation behavior of nesting waterfowl and changes in daily weather patterns (Afton 1980, Eichholz and Sedinger 1999, Poussart et al. 2001), and predation of goose eggs is expected to be negatively correlated with nest attentiveness (Afton and Paulus 1992). Due to the large size and aggressive behavior of incubating swans, we expected that total nest failures were mainly a result of depredation by bears and that partial clutch losses resulted from depredation by other predators. Because our analysis of egg survival included only data from eggs in successful nests, we attribute reductions in egg survival to depredation by avian and small mammalian predators. Incubating swans are highly visible, and unattended nests are relatively inconspicuous; therefore, we suspect that bears were more likely to detect a nest in the presence of incubating swans. However, in the absence of incubating adults, there is a large suite of predators capable of depredating swan eggs: gulls (*Larus spp.*), common ravens (*Corvus corax*), and red fox (*Vulpes vulpes*; Monda et al. 1994). Therefore, we expected depredation of eggs to be negatively related to nest attendance, and depredation of nests to be positively related to nest attendance. Incubation constancy of nesting swans and geese is expected to increase as temperatures decline and in association with rain events (Eichholz and Sedinger 1999, Poussart et al. 2001). We speculate that nest DSP was lower during periods of colder temperatures and precipitation events because high rates of nest attendance increased the probability of detection by bears. In contrast, egg DSP was higher during periods of colder temperatures because increased nest attentiveness reduced the probability of predation by predators other than bears. Furthermore, although our results indicate a negative

relationship between egg DSP and precipitation, we suggest that egg DSP was actually higher during precipitation events as a result of increased nest attentiveness, but decreased immediately after precipitation events when nest attentiveness likely decreased (Afton and Paulus 1992).

Inclement weather challenges the ability of young waterfowl to thermoregulate as a result of increased energetic demands and their available lipid reserves (Lesage and Gauthier 1997). We expected cygnet survival probabilities to be negatively related to temperature and precipitation. The lower critical temperature for greater snow goose goslings is 15 °C (Ratté 1998), and mean ambient temperatures during the brood-rearing period on our study area were below this temperature >99% of the time. Because energetic costs to young waterfowl are directly related to temperature (Beasley and Ankney 1992) we expected survival of cygnets to decrease as a result of cold temperatures. Contrary to our hypotheses and several studies conducted on pre-fledged waterfowl (i.e., Schmutz et al. 2001, Traylor and Alisauskas 2006), our models indicated considerable support for a negative relationship between cygnet DSP and temperature. Fortin et al. (2000) found that greater snow goose goslings spent longer periods of time separate from adults during warmer temperatures, and spent more time brooding during colder temperatures. Therefore, distance of cygnets from adults may put them at greater risk of predation. Precipitation has been linked to mortality of goslings (Schmutz et al. 2001, Kostin and Mooij 1995), and we were surprised that our results did not support a precipitation effect. We may not have detected a precipitation effect as a result of the length of our revisit intervals or as a result of our model structure that predicted a

precipitation effect on the day of precipitation. If mortality as a result of precipitation was delayed, the effect may not have been detected by our models.

### **Additional Sources of Variation in Cygnet Survival**

Potential predators of cygnets on our study area included red foxes, bald eagles (*Haliaeetus leucocephalus*), glaucous-winged gulls (*Larus glaucescens*), gyrfalcons (*Falco rusticolus*), and brown bears (C. P. Dau, U. S. Fish and Wildlife Service, personal observation). Although we lack data on cause-specific mortality of cygnets, we observed bald eagles preying on young cygnets that were still in the vicinity of the nest. Similar to the findings of other studies, our data indicated increased survival probabilities with increasing age of cygnets (Lensink 1973, Brown and Brown 2002). Increased DSP with increasing age is a result of increasing size (larger young have fewer potential predators) and increasing ability to thermoregulate, forage, and avoid predators (Sedinger 1992).

Plastic neckbands are known to reduce the survival rate of marked geese (Schmutz and Morse 2000, Alisauskas and Lindberg 2002), and Menu et al. (2001) documented reduced survival probabilities of young geese shortly after banding. Our models predicted a reduction of 0.01 in DSP for each day post capture, and consequently, fledging probability was positively related to age at the time of neckbanding. The probability of fledging for a cygnet neckbanded at ages 46 and 55 days was 16.9% and 6.3% lower, respectively, than a cygnet that was not neckbanded. Prior to banding, family groups appeared to have small home ranges and were often observed consistently on a single wetland. However, after banding, it was common for family groups to travel considerable distances over land to new locations. We suspect that in addition to

potential mortality risks directly associated with the presence of neckbands, stress induced by capture events and disturbance induced dispersal following banding likely resulted in reduced survival probabilities of neckbanded cygnets (Samuel et al. 1990).

### **Long-term Variation in Productivity**

The Izembek population exhibited non-migratory behavior during most winters (1980–96) but during the winters of 1987–89 a large proportion of the population migrated out of Alaska to the Pacific Northwest (Dau and Sarvis 2002). In years immediately following migration events, the abundance of swans on the Izembek breeding grounds declined by 37% (Dau and Sarvis 2002). Additionally, the total number of nest attempts during 1988–96, following migration events, was 59% lower than the number of nest attempts prior to migration events during 1980–87. Although densities of nesting swans in remote areas were reduced following migration events, rates of productivity were similar before and after migration events. In contrast, swans on the road system nested in high densities and exhibited high levels of reproductive success prior to migration events, but nested in low densities and exhibited low levels of reproductive success following migration events. The number of documented nest attempts on the road system averaged 8.3 per year during 1980–87 (range: 4–13), but only 2.2 per year during 1988–96 (range: 1–3). Additionally, only 4 nests were known to successfully hatch cygnets on the road system post-migration, as compared to 38 pre-migration. Dau and Sarvis (2002) attribute the reduction of nesting pairs following the migration events to permanent emigration. Therefore, the swans that nested in the area following dispersal events may have had lower reproductive success because they were

younger and less experienced. However, because the number of nest attempts on the road system remained low, additional factors may be responsible for the observed variation in reproductive success. Bear harvest was discontinued or highly restricted on the road system after 1984, allowing bear densities to increase (Dau 1989). The extent of the increase was not documented, but it is possible that increased bear densities on the road system after migration events resulted in reduced levels of productivity.

Furthermore, as a result of low reproductive success on the road system, breeding pairs may have been reluctant to nest there in subsequent years (Johnson et al. 1992, Haas 1998). Current reports indicate that bear densities on the road system are similar to those in remote areas and that the number of annual nest attempts on the road system are similar to those observed during 1988–96 (K. M. Sowl, U.S. Fish and Wildlife Service, personal observation).

### **Implications for the Izembek Population**

Fluctuations in the number of breeding pairs (range: 23–86) and population abundance (range: 57–266) on the Izembek breeding grounds between 1980 and 2006 indicate population instability (Dau and Sarvis 2002, Meixell 2007). The influence of environmental and demographic stochasticity on population dynamics is negatively correlated with population size, such that small populations are more prone and sensitive to fluctuations in abundance, and ultimately, their risk of extinction is greater than that of large populations (Lande et al. 2003). Furthermore, stochastic variation in demographic parameters alone, even without changes in mean values, is expected to result in reduced long-term population growth rates (Tuljapurkar 1982). Meixell (2007) reported mean

annual apparent survival rates of 0.67 for adult (>2 years), and 0.49 for immature (<3 years) swans neck-collared on the Izembek breeding grounds during 1978–87. These estimates are lower than previously reported for swan survival across species and populations (Bart et al. 1991), and we suspect that this level of productivity is of insufficient magnitude to maintain a constant population size. Management actions that increase levels of productivity, even among long-lived species, are expected to positively influence short-term population growth rates, and may lead to desirable increases in long-term abundance (Koons et al. 2006). Furthermore, reproductive success in previous nesting attempts is thought to be a primary factor influencing rates of breeding dispersal in waterfowl (Johnson et al. 1992), and Meixell (2007) suggested that emigration was a primary source of losses to the Izembek population. Therefore, management to increase productivity of Izembek swans may also act to reduce rates of breeding dispersal, and thereby moderate fluctuations in population abundance.

## **MANAGEMENT IMPLICATIONS**

Our estimates of tundra swan nest survival in remote areas on our study area were lower than those reported elsewhere in Alaska, and negative relationships between nesting success and brown bear densities suggest that depredation by bears is a primary determinant of tundra swan reproductive success. Our results indicate that management actions to reduce bear abundance in the past likely had unintended positive effects on tundra swan productivity. Therefore, we suggest that future reductions in bear densities

would likely result in increased rates of tundra swan productivity and recommend that the goals and objectives of bear management take into consideration the effects of bear density on tundra swan population dynamics. Furthermore, management to increase levels of productivity may help to limit fluctuations in population abundance by increasing recruitment of young to the population and reducing rates of breeding dispersal.

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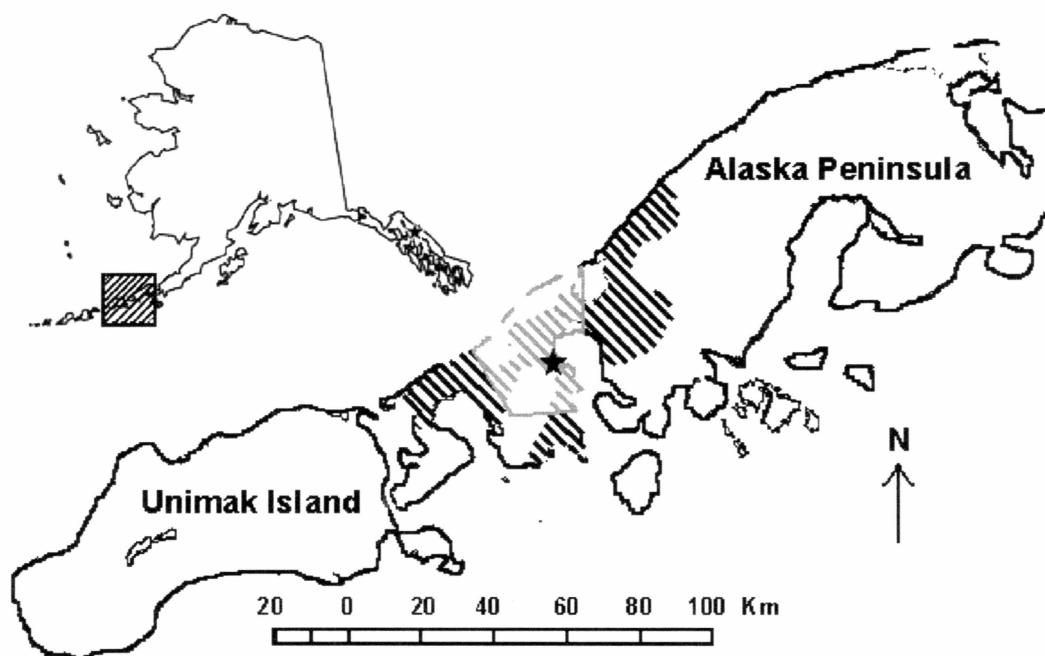


Figure 1. Location of study site on and adjacent to Izembek National Wildlife Refuge, Alaska Peninsula, USA. Shaded region represents the study area, gray-shaded region represents the Cold Bay Road System, and the star represents the City of Cold Bay.

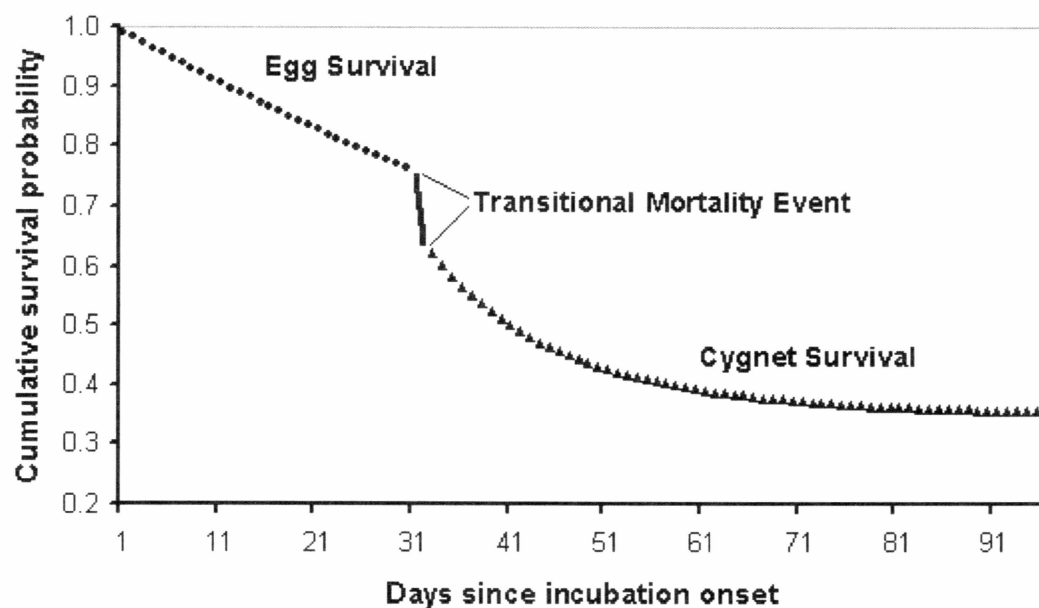


Figure 2. Cumulative survival probability of tundra swan eggs and cygnets on the lower Alaska Peninsula, USA. Egg survival rates are from eggs in successful nests using average values for temperature and precipitation. Transitional mortality event (TME) is an intercept adjustment applied to the hatch date that represents unknown life stage mortality between last visit pre-hatch and first visit post-hatch. Cygnet survival is represented for average effects of year, age, and temperature.

Table 1. Models of Daily Survival Probability (DSP) of tundra swan nests on the lower Alaska Peninsula, USA, 1980–1987. Models are ranked by Akaike’s Information Criterion adjusted for small sample size (AICc).

DSP model <sup>a</sup>	K <sup>b</sup>	AICc	$\Delta$ AICc	$w_i^c$
Temporal covariates only <sup>d</sup>				
year * T	16	748.18	0	0.64
year + T	9	752.05	3.87	0.09
All covariates <sup>e</sup>				
year + T + road	10	723.11	0	0.20
(year * T) + road	17	723.79	0.68	0.14
year + T + road + precip	11	724.09	0.98	0.12
(year * T) + road + precip	18	724.43	1.32	0.10
(year * T) + road + temp	18	724.84	1.72	0.08
year + T + road + temp	11	724.93	1.81	0.08
(year * T) + road + temp + precip	19	725.04	1.92	0.08
year + T + road + temp + precip	12	725.71	2.59	0.05
road + temp + precip	4	725.71	2.59	0.05
road + temp	3	726.19	3.08	0.04
road + precip	3	726.91	3.79	0.03
year * T <sup>f</sup>	16	748.18	25.07	0.00

Table 1 continued.

<sup>a</sup> Abbreviations: year = 1980–87; T = linear time trend; road = road system (depicts high and low bear density areas); precip = daily precipitation; temp = daily minimum temperature. The + between variables indicates an additive effect; the \* denotes interaction.

<sup>b</sup> Number of parameters.

<sup>c</sup> AICc model weight.

<sup>d</sup> Top approximating models with parameters of temporal variation only ( $\Delta\text{AICc} < 4.0$ ); used for addition of specific covariates.

<sup>e</sup> Top approximating models from full model set ( $\Delta\text{AICc} < 4.0$ ).

<sup>f</sup> Top approximating model with parameters of temporal variation only; inserted for comparison.

Table 2. Model-averaged tundra swan nest survival probability ( $\hat{S}$ ), on and off the road system, on the lower Alaska Peninsula, USA, 1980–1987.

Year	Nest location					
	On road system <sup>a</sup>			Remote areas <sup>b</sup>		
	$\hat{S}$	$\hat{SE}$	95% CI	$\hat{S}$	$\hat{SE}$	95% CI
1980	0.76	0.09	0.59, 0.93	0.34	0.12	0.11, 0.58
1981	0.61	0.13	0.36, 0.86	0.16	0.09	0.00, 0.33
1982	0.76	0.08	0.60, 0.92	0.35	0.11	0.14, 0.57
1983	0.76	0.10	0.57, 0.95	0.35	0.15	0.05, 0.65
1984	0.93	0.04	0.84, 1.00	0.76	0.13	0.50, 1.00
1985	0.77	0.08	0.61, 0.93	0.37	0.11	0.14, 0.59
1986	0.80	0.07	0.67, 0.93	0.42	0.09	0.25, 0.59
1987	0.75	0.08	0.59, 0.91	0.32	0.09	0.14, 0.50

<sup>a</sup> Geographic area (200 km<sup>2</sup>) with low bear densities.

<sup>b</sup> Geographic area (871 km<sup>2</sup>) with high bear densities.

Table 3. Models of Daily Survival Probability (DSP) of tundra swan eggs and cygnets on the lower Alaska Peninsula, USA, 1980–1987. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc).

DSP model <sup>a</sup>	K <sup>b</sup>	AICc	$\Delta$ AICc	$w_i^c$
Temporal covariates only <sup>d</sup>				
EGG <sub>T</sub> TME <sub>year</sub> CYG <sub>year + age</sub>	19	2201.44	0.00	0.50
EGG <sub>T</sub> TME CYG <sub>year * age</sub>	19	2202.70	1.27	0.27
EGG <sub>T</sub> TME <sub>year</sub> CYG <sub>year * age</sub>	26	2203.11	1.67	0.22
EGG <sub>T</sub> TME CYG <sub>year + age</sub>	12	2209.36	7.92	0.01
All covariates <sup>e</sup>				
EGG <sub>temp + precip</sub> TME CYG <sub>year + age + temp + collar</sub>	15	2164.44	0.00	0.68
EGG <sub>temp + precip</sub> TME <sub>year</sub> CYG <sub>year + age + temp + collar</sub>	22	2166.65	2.21	0.22
EGG <sub>temp + precip</sub> TME CYG <sub>(year * age) + temp + collar</sub>	22	2168.39	3.95	0.09
EGG <sub>T</sub> TME <sub>year</sub> CYG <sub>year + age</sub> <sup>f</sup>	19	2201.44	36.99	0.00

<sup>a</sup> Abbreviations: T = linear time trend; TME = transitional mortality event (represents unknown life stage mortality over hatching interval); year = 1980–87; temp = daily minimum temperature, precip = daily precipitation; collar = plastic neckband. The + between variables indicates an additive effect; the \* denotes interaction.

Table 3 continued.

<sup>b</sup> Number of parameters.

<sup>c</sup> AICc model weight.

<sup>d</sup> Top approximating models with parameters of temporal variation only ( $\Delta\text{AICc} < 8.0$ );  
used for addition of specific covariates.

<sup>e</sup> Top approximating models from full model set ( $\Delta\text{AICc} < 4.0$ ).

<sup>f</sup> Top approximating model with parameters of temporal variation only; inserted for  
comparison.

Table 4. Models of Daily Survival Probability (DSP) of tundra swan nests and broods on the lower Alaska Peninsula, USA, 1980–1996. Models are ranked by Akaike's Information Criterion adjusted for small sample size (AICc).

DSP model <sup>a</sup>	K <sup>b</sup>	AICc	$\Delta$ AICc	$w_i^c$
Temporal covariates only <sup>d</sup>				
YEAR <sup>2</sup> + T	4	1768.84	0.00	0.41
year + T	18	1770.07	1.23	0.22
YEAR <sup>2</sup> + TT	5	1770.37	1.53	0.19
year + TT	19	1771.96	3.12	0.09
migration + T	3	1772.08	3.24	0.08
All covariates <sup>e</sup>				
(migration * road) + T + sdprecip	6	1733.43	0.00	0.45
(migration * road) + T + sdprecip + mintemp	7	1734.03	0.60	0.34
(migration * road) + T	5	1736.02	2.58	0.12
(migration * road) + T + mintemp	6	1736.80	3.37	0.08
YEAR <sup>2</sup> + T <sup>f</sup>	4	1768.84	35.41	0.00

<sup>a</sup> Survival is not partitioned among life stages (i.e., nests and broods). Abbreviations: year = 1980–96; YEAR<sup>2</sup> = quadratic year trend; T = linear time trend; migration = year divided into 2 groups (1980–87, before onset of major migration events and 1988–96, after onset of major migration events); TT = quadratic time trend; road = road system (depicts areas of differing bear harvest regulations); sdprecip = standard deviation of precipitation; antemp = number of days with temperatures below 2 °C. The + between variables indicates an additive effect; the \* denotes interaction.



Table 4 continued.

<sup>b</sup> Number of parameters.

<sup>c</sup> AICc model weight.

<sup>d</sup> Top approximating models with parameters of temporal variation only ( $\Delta\text{AICc} < 4.0$ );  
used for addition of specific covariates.

<sup>e</sup> Top approximating models from full model set ( $\Delta\text{AICc} < 4.0$ ).

<sup>f</sup> Top approximating model with parameters of temporal variation only; inserted for  
comparison.

## CHAPTER 2

### AGE-SPECIFIC SURVIVAL OF TUNDRA SWANS ALONG THE LOWER ALASKA PENINSULA<sup>1</sup>

**Abstract:** We neck-collared tundra swans on and adjacent to Izembek National Wildlife Refuge on the Lower Alaska Peninsula during late summer from 1978 to 1996. We used recapture, resighting, and recovery data to estimate collar loss rates, annual apparent survival rates, and other demographic parameters for the years 1978–1989. Annual collar loss rates were higher for adult males fitted with the thinner collar type (0.34) or the thicker collar type (0.15) than for other swans (thinner: 0.10, thicker: 0.04). Estimates of apparent survival probability were higher for adults (mean = 0.67, SE = 0.07) than immatures (mean = 0.49, SE = 0.08) and varied among years for both age classes (adult range: 0.44–0.95, immature range: 0.25–0.90). Using variance-components analysis, we estimated that 90% of annual variation in estimates of apparent survival was biological variation for both adults and immatures. To assess effects of permanent emigration among age and breeding classes, we conducted a post-hoc analysis in which we included only encounter histories of swans known to breed on our study area. Resulting estimates of apparent survival were generally higher but still varied by

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year (range: 0.51–1.0, SE: 0.09–0.16) and indicated that emigration likely occurred in breeding swans. We suggest that reductions in apparent survival probability were primarily influenced by high and variable rates of permanent emigration, and that immigration by swans from elsewhere may be important in sustaining a breeding population on our study area.

**Key words:** Alaska, Alaska Peninsula, apparent survival, *Cygnus columbianus*, emigration, neck collar, population dynamics, collar loss, tundra swan.

## INTRODUCTION

Tundra swans (*Cygnus columbianus columbianus*) in North America are managed as 2 distinct populations. The Western Population (WP) breeds along the western coast of Alaska from Point Hope south to the Aleutian Islands and winters primarily in California, Utah, and the Pacific Northwest (Bellrose 1980, Bart et al. 1991a). The Eastern Population (EP) breeds along the Arctic coast of Alaska and Canada east of Point Hope and winters primarily in Maryland and North Carolina (Limpert et al. 1991). Tundra swans of the lower Alaska Peninsula breed at the southern extremity of the WP range and exhibit unique non-migratory behavior (Dau and Sarvis 2002). Unlike their counterparts in more northern latitudes, tundra swans neck-collared on and adjacent to Izembek National Wildlife Refuge (Izembek NWR) during 1978–1996 wintered in Alaska and were observed in large concentrations on nearby Unimak Island (Dau and

Sarvis 2002; Fig. 1). This unique non-migratory behavior combined with potential morphometric differences (C. P. Dau, U.S. Fish and Wildlife Service and J. M. Pearce, U.S. Geological Survey, unpublished data), provides evidence that swans on and adjacent to Izembek NWR (hereafter: Izembek population) may represent a population that is functionally isolated from other WP swans. However, variation in the number of Izembek swans observed outside Alaska during winter is puzzling. Some proportion of collared individuals were observed outside Alaska in most winters during 1980–1996, and resighting data indicate that during the winters of 1987–1989 large proportions of the population migrated to traditional WP wintering areas (Dau and Sarvis 2002). Breeding-ground population abundance during years immediately following these migration events was reduced to previously unobserved lows but returned to pre-migration levels by 1991 (Dau and Sarvis 2002). As part of an ongoing study to improve our understanding of the ecology of Izembek tundra swans and to identify factors affecting their population growth rate, we analyzed 11 years of capture-recapture data to estimate demographic parameters of collared post-fledging swans.

In stable populations of long-lived waterfowl species (i.e., swans and geese), low rates of productivity are balanced by high survival rates (Charlesworth 1994). As a result, population growth rates for such species are likely to be influenced more by adult survival than other demographic parameters (Lebreton and Clobert 1991, Heppell et al. 2000). Therefore, understanding variation in survival rates is important for understanding factors behind fluctuations in population abundance for long-lived species. Permanent emigration and mortality are confounded in estimates of apparent survival;

therefore, permanent emigration results in estimates of apparent survival that are lower than estimates of true survival (Sandercock 2006). However, management is generally focused on population abundance, and the establishment of management priorities considers effects on population growth rate. Therefore, knowledge about losses to the population, regardless of the source, is important for identifying management priorities and understanding population dynamics. We used recapture, recovery, and observation data from tundra swans neck-collared on and adjacent to Izembek NWR to: 1) obtain annual estimates of apparent survival probability, 2) examine variation in apparent survival and collar retention rates among age- and sex classes, and 3) provide recommendations for management of swans breeding on the lower Alaska Peninsula.

## **STUDY AREA**

We conducted our study on and adjacent to Izembek National Wildlife Refuge (55°10'N, 162°40'W) on the lower Alaska Peninsula (Fig. 1). Tundra swan habitat was characterized by low elevation coastal wetlands surrounded by ericaceous uplands. The 1,071-km<sup>2</sup> study area is bordered by the Pacific Ocean, the Bering Sea, and volcanic mountains. During winter months, swans often congregated on coastal lagoons of Unimak Island where geothermal activity provided ice-free habitat (Fig. 1). The study area was described in detail by Dau and Sarvis (2002).

## METHODS

### Data Collection

We conducted an annual aerial population census in late May and early June during 1998–2000 using methods described by Dau and Sarvis (2002). We surveyed all available swan habitat on our study area and recorded observations of swans as singles, pairs, and flocks.

We captured flightless cygnets and molting adult swans with dip nets from a taxiing floatplane, small boats, or by hand during July and August (1978–88, 1990–95). Family groups were usually captured individually while failed and non-breeding molting adults were congregated in flocks of up to 40 individuals. We marked adults and cygnets with plastic neck collars and tarsus bands with engraved alphanumeric characters and U.S. Fish and Wildlife Service metal tarsus bands. Beginning in 1981, we marked captured swans with collars that were thicker and presumably more durable than those used in previous years. Upon capture of previously marked swans, we assessed the physical condition of collars and replaced those that were worn or lost. We used cloacal examination to determine sex and plumage characteristics to classify birds as hatch-year (HY), second-year (SY), or after-second-year (ASY; Dau and Sarvis 2002). We obtained resightings of collared swans on the breeding grounds (April–September, 1978–88) and on Unimak Island (November–March, 1978–83, 85, 86). Additionally, we acquired live resighting and dead recovery data for swans encountered outside of Alaska through state

and national wildlife refuge staff (>90%), independent observers, and the Bird Banding Laboratory, U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.

## **Data Analysis**

*Population Abundance.* To assess population status and identify potential long-term trends in abundance, we used simple linear regression (SAS Institute 1990) to analyze annual census data collected during 1980–1996 (Dau and Sarvis 2002) and 1998–2006.

*Apparent Survival.* We obtained maximum likelihood estimates of demographic parameters using Program TLSURVIV in which multistate models were extended to allow the combination of recaptures, resightings, and recoveries during both closed and open sampling periods, as described by Conn et al. (2004). Program TLSURVIV produces direct estimates of collar loss rates and corrects estimates of demographic parameters for potential bias resulting from collar loss (Conn et al. 2004). We constructed the model such that closed sampling periods occurred during late summer (17 Jul–2 Sep) and corresponded to the period when swans were captured and marked (Fig. 2). In addition to initial releases, encounters during closed sampling periods included resightings or recaptures of marked birds on our study area. Open sampling periods were the intervals between successive closed sampling periods and included resightings and recoveries from any location (i.e., within or outside of Alaska). While births, deaths, immigration, and emigration could occur during open sampling periods, the study population was assumed to be stable in size during closed sampling periods.

Collar loss was estimated as the probability of state transition in a multistate framework, where state variables included: 1) collared ( $s$ ) and 2) leg-banded-only ( $t$ ). Estimates of detection probability correspond to the time period between successive open intervals (17 Jul–2 Sep), and the remaining parameters correspond to the time period between successive closed sampling periods (3 Sep–16 Jul; Conn et al. 2004; Fig. 2). We refer to year-specific estimates by the year in which the interval began.

Within the TLSURVIV model framework, state transitions are unidirectional such that following collar loss, individuals are not allowed to transition back to the collared state (Conn et al. 2004). Therefore, to allow the inclusion of encounter data for re-collared individuals, we identified birds fitted with replacement collars as losses on capture in the relevant closed sampling period such that their re-release began a new encounter history. A key assumption of multistate models is that state transitions occur immediately before or immediately after closed sampling periods (Joe and Pollock 2002). Examination of our collar loss data indicated that the highest incidence of collar loss occurred between mid-winter and summer. Because Program TLSURVIV is formulated such that state transition is set to occur immediately following release in closed sampling periods, we were required to manipulate encounter histories to allow state transition to occur immediately before closed sampling periods, so as to avoid eliminating a large sample of winter resightings (i.e., birds that were observed during winter, but captured without collars present during subsequent summers). Thus, to correctly partition timing of collar loss, we added an additional artificial closed and open interval to each year. In the first open interval, we constrained collar loss to be 0.0 and estimated all other



parameters. In the second open interval we estimated collar loss, but constrained survival to be 1.0 and the remaining parameters to be 0.0 (Fig. 2). Therefore, estimates of collar loss rates correspond to original open sampling intervals. Additional intervals are considered to be instantaneous, were added simply to reformulate the model, and only affect interpretation of parameter estimates in regards to timing of state transition. Therefore, we define and interpret parameters in accordance with 1 closed sampling interval and 1 open sampling interval per year:

$\psi_i^{st}$  (collar loss probability) = the probability that an animal alive and in the collared state  $s$  in closed sample  $i$  lost its collar and transferred to the leg-banded-only state  $t$  immediately prior to  $i + 1$ .

$\phi_i$  (apparent survival probability) = the probability that an animal alive in closed sample  $i$  survived to  $i + 1$  and did not permanently emigrate from the study area.

$p_i$  (detection probability) = the probability that an animal alive during closed sample  $i$  was encountered during closed sample  $i$ .

$\lambda_i$  (recovery rate) = the probability that an animal alive in closed sample  $i$  is reported dead between  $i$  and  $i + 1$ .

$R_i$  (resighting rate) = the probability that an animal alive in closed samples  $i$  and  $i + 1$  was encountered alive between  $i$  and  $i + 1$ .

$R'_i$  = the probability that an animal alive in closed sample  $i$  was encountered alive between  $i$  and  $i + 1$  but subsequently died without being reported between  $i$  and  $i + 1$ . This parameter only aids in the unbiased estimation of other parameters and has no direct biological interpretation.

A number of constraints were necessary to permit parameter identifiability. Time dependence on  $R'$  resulted in a strong covariance structure among parameters, so we constrained  $R'$  to be constant. Additionally, we constrained all  $R$  and  $R'$  parameters to be 0.0 for the leg-banded-only state during open sampling periods because only birds in the collared state could be resighted in open intervals. To estimate state-specific survival, the model framework in Program TLSURVIV requires that a substantial portion of individuals are released in the leg-banded-only state (Conn et al. 2004). Because our data did not meet this requirement, we constrained all parameters (except  $\psi$ ) to be equal among states. Additionally, to permit parameter identifiability in the last time period, we constrained the last 2 years to be equal, and therefore only report parameter estimates for years prior to 1987. With the exceptions mentioned above, we made the same assumptions and followed the same analytical procedures as Conn et al. (2004).

We developed 30 *a priori* models under an information theoretic approach (Burnham and Anderson 2002) to compare competing hypotheses about variation in tundra swan demographic parameters. To avoid over fitting the data and because some parameters were data-limited, we considered only additive interactions among covariates and limited year-specific model structures to  $\phi$  and  $p$ . We allowed  $\phi$  to vary by sex, age class (immature and ASY or HY, SY, and ASY), year, and all possible 2-way additive models with sex, age, and year;  $p$  was allowed to vary by year and age. We expected collar retention rates to differ among collar types. Furthermore, previous studies reported lower rates of collar retention for adult males (Allen et al. 1991, Nichols et al. 1992). Therefore, we structured  $\psi$  to produce differential estimates by collar type

(TYPE I: 1978–1980; TYPE II: 1981–1988) and assessed an additive effect of age and sex by grouping birds as ASY MALES and OTHER. We expected resighting rates to be considerably higher in years when weather permitted collar surveys on Unimak Island. Therefore, we structured  $R$  to produce separate estimates for years with Unimak surveys (SURVEY, 1978-83, 1985-86) and those without (NOSURVEY, 1984, 1987–88). We constrained  $\lambda$  to be time constant because our dataset contained few dead recoveries. We selected the most parsimonious model using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) and model weights ( $w_i$ ; Burnham and Anderson 2002). We calculated average estimates of apparent survival across all years by weighting year-specific estimates by the inverse of sampling variances (Burnham et al. 1987).

*Process Variation.* We used an iterative approach to obtain estimates of temporal variance in our year-specific estimates of apparent survival (Burnham et al. 1987), where total variance ( $\sigma^2_{total}$ ) is the sum of process ( $\sigma^2_{process}$ ) and sampling ( $\sigma^2_{sampling}$ ) variance. Process variation is defined as true biological variation, and sampling variation is a measure of uncertainty associated with parameter estimates as a result of sample information (Gould and Nichols 1998).

*Post-hoc Analysis.* Because our estimates of apparent survival were highly variable and surprisingly low in many years, we suspected that our marked sample might have contained transients (i.e., members of some other population that temporarily immigrated to our study area). Transients are not available for subsequent encounters and therefore have an effective survival probability of 0.0 (Loery et al. 1997, Pradel et al. 1997). Consequently, the occurrence of transients in our marked sample would have

resulted in estimates of apparent survival that were negatively biased relative to the Izembek-breeding population (Pradel et al. 1997, Cilimburg et al. 2002). A summary of the data, 1978–1986, revealed that 2 of 63 marked, known breeders and 16 of 302 marked, non- or unknown breeders were observed outside of Alaska. Both of the known breeders, but only 4 of the unknown breeders were encountered on our study area in subsequent years, suggesting the prevalence of transients in our marked sample. Therefore, in an attempt to assess the degree to which permanent emigration by non-breeders affected our estimates of apparent survival, we conducted a post-hoc analysis in which we only considered adults that were known to breed on our study area between 1978 and 1987. We developed a set of 3 models where  $\phi$  was constant or varied by year or sex. We constrained  $p$  to be constant, modeled  $\psi$  by collar type with an additive effect of sex, and constrained remaining parameters as described above.

## RESULTS

### Population Abundance

The total number of swans observed during spring on our study area during 1980–2006 (mean = 180, SD = 61.23) fluctuated from a high in 1985 (266) to a low in 2002 (57; Fig. 3). Our model predicted a negative linear trend in abundance ( $y = 9782.82 + -4.82 * \text{year}$ ,  $R^2 = 0.38$ ,  $p < 0.05$ ,  $df = 25$ ).

## Apparent Survival

We neck-collared 490 swans (males = 236, females = 254; 1978–1988) and re-collared 27 individuals to replace lost or damaged collars. Swans marked with replacement collars were treated as new individuals upon release, resulting in a total of 519 encounter histories. Of these, 276 individuals were encountered alive during open sampling periods and 90 were encountered (includes resightings and recaptures) during closed sampling periods on our study area (Table 1). Additionally, 43 individuals were encountered outside of Alaska and 11 of these were known to return to our study area in subsequent years. We obtained reports of 13 dead recoveries (9 outside Alaska, 4 within Alaska), 10 of which occurred in the last two winters of our study. Of 20 individuals captured without their collars, 14 were ASY males at the time of marking (Table 2).

Our top-approximating model ( $w_i = 0.66$ ) allowed  $\phi$  to vary by year with an additive effect of age (immature and ASY) and allowed  $p$  to vary by age (HY, SY, ASY; Table 3). We found limited support for a 3-age-class effect on survival ( $\Delta AIC = 1.66$ ) and did not find evidence supporting an effect of sex on survival (Table 3). Apparent survival estimates were higher for ASY swans (mean = 0.67,  $\hat{SE} : 0.07$ ) than for immatures (mean = 0.49,  $\hat{SE} = 0.08$ ; Fig. 4). Detection probability was lowest for SY swans (0.08,  $\hat{SE} = 0.04$ ) and higher for HY (0.26,  $\hat{SE} = 0.07$ ) and ASY (0.28,  $\hat{SE} = 0.03$ ) swans. Collar loss rates varied between collar types and were higher for ASY males (TYPE I: 0.34,  $\hat{SE} = 0.10$ ; TYPE II: 0.15,  $\hat{SE} = 0.49$ ) than for other swans (TYPE I: 0.10,  $\hat{SE} = 0.05$ ; TYPE II: 0.04,  $\hat{SE} = 0.02$ ). The resighting rate was 0.78 ( $\hat{SE} = 0.03$ ) during years that winter surveys were conducted on Unimak Island and 0.42

( $\hat{SE} = 0.07$ ) for years without Unimak surveys. The recovery rate was 0.03 ( $\hat{SE} = 0.01$ ).

### Process Variation

Total variation in year-specific estimates of apparent survival was 0.21 for ASY swans and 0.25 for immature swans. Our estimates of process variation were 0.19 (CI: 0.13–0.41) for ASY swans and 0.23 (CI: 0.14–0.50) for immature swans. Therefore, we estimate that true biological variation accounted for 92.5% (CI: 61.0%–100.0%) and 89.9% (CI: 60.3%–100%) of total variation for ASY and immature swans, respectively.

### Post-hoc Analysis

We analyzed 92 encounter histories of 73 adult swans known to breed on our study area sometime during 1978–1987. Our top approximating model ( $w_i = 1.0$ ) allowed  $\varphi$  to vary by year (Table 4). We were forced to constrain  $\varphi$  to be 1.0 for the years 1978–1980 because no mortalities occurred in those years. Mean apparent survival was 0.81 ( $\hat{SE} = 0.04$ ), and ranged from 0.51 ( $\hat{SE} = 0.11$ ) to 1.0 (Fig. 5). Collar loss rates were higher for males (TYPE I: 0.25,  $\hat{SE} = 0.12$ ; TYPE II: 0.12,  $\hat{SE} = 0.05$ ) than for females (TYPE I: 0.05,  $\hat{SE} = 0.04$ ; TYPE II: 0.02,  $\hat{SE} = 0.02$ ).  $R$  was 0.88 ( $\hat{SE} = 0.04$ ) during years that winter surveys were conducted on Unimak Island and 0.65 ( $\hat{SE} = 0.12$ ) for years without Unimak surveys; detection probability was 0.43 ( $\hat{SE} = 0.06$ ).

## DISCUSSION

### Permanent Emigration

Our estimates of apparent survival were highly variable, and in 5 years estimates were lower than previously observed for swan survival across species (Bart et al. 1991b). Such high and variable rates of mortality appear unrealistic given our knowledge of tundra swan life history (Krementz et al. 1997). Therefore, we suggest that some proportion of marked birds probably emigrated from our study area at rates that varied among years. This may have been due to marked transients that were not truly associated with our population (Pradel et al. 1997), or to residents of our population that subsequently dispersed from our study area (Cilimburg et al. 2002). We assessed the prevalence of transients in our marked sample by estimating apparent survival separately for known breeders, under the assumption that breeders were residents of the population. Mean apparent survival for known breeders was higher (0.81) than that of the entire marked sample of ASY birds (0.67), and year-specific estimates were higher in all but one year. Because combined rates of emigration and mortality were lower for known breeders than for all marked adults, it is likely that our marked sample contained a variable number of transients. However, estimates varied considerably among years (range: 0.51–1.0) and were below 0.65 in 3 years, indicating that permanent emigration was also likely prevalent among known breeders. Therefore, we suspect that some annual variation in our estimates of apparent survival was a result of marked transients, but that some proportion of swans in all age- and breeding classes dispersed from the

study area, and that permanent emigration was an important source of loss to the population.

Reproductive success in previous nesting attempts is thought to be a primary factor influencing rates of breeding dispersal in waterfowl and other birds (Johnson et al. 1992, Haas 1998). Meixell (2007) suggested that high rates of nest depredation by brown bears were responsible for low levels of productivity on the Izembek breeding grounds. Therefore, unfavorable reproductive success and high predator densities may represent important factors influencing rates of permanent emigration among adult swans from the Izembek breeding grounds (Johnson et al. 1992, Meixell 2007).

### **Age-specific Variation in Apparent Survival**

Among studies of swan survival across species and populations, estimates of apparent survival for immature swans were lower than those for adults and were within the range of 70–90% of adult rates (Bart et al. 1991b). Consistent with these findings, our estimates of apparent survival for immature swans were lower and, on average, 73% of the adult rate. We lack information on dead recoveries within Alaska; however, 31% of 26 immatures, but only 3% of 31 adults encountered outside of Alaska were recovered dead, indicating that rates of mortality for migrating immatures were higher than that of migrating adults. Rates of dispersal among waterfowl are generally higher for younger birds; and among a sedentary population of mute swans in Britain, breeding swans were highly site-faithful, while young swans dispersed at high rates (Anderson et al. 1992). Therefore, our observed differences in estimates of apparent survival may have resulted from variation in true survival among age classes or variation in rates of dispersal among



age classes (Greenwood and Harvey 1982, Blums et al. 2003, Lebreton et al. 2003), and we suspect that both factors influenced our estimates of apparent survival.

### **Variation in Survival among Populations**

Life history theory predicts that swans, a large bodied waterfowl species with relatively low levels of reproductive success and investment, should exhibit relatively high and stable rates of annual survival (Charlesworth 1994, Krementz et al. 1997). Furthermore, among long-lived species, adult survival is expected to be the most influential demographic parameter on population growth rates (Lebreton and Clobert 1991, Heppell et al. 2000). Our mean estimate of adult apparent survival ( $0.67$ ,  $\hat{SE} = 0.07$ ) and our year-specific estimates for most years (range:  $0.44$ – $0.95$ ), are substantially lower than that estimated from a study of 5,963 EP swans neck-collared during 1966–1990 on Maryland and North Carolina wintering grounds ( $0.92$ ,  $\hat{SE} = 0.04$ ; Nichols et al. 1992). Furthermore, our estimates are lower than those reported across species and populations of swans (Bart et al. 1991a). However, 6-month survival estimates from a separate analysis of 416 tundra swans neck-collared on their Alaskan breeding grounds (1971–1974) and subsequently resighted on east coast wintering grounds, (males =  $0.81$ ,  $\hat{SE} = 0.09$ ; females =  $0.52$ ,  $\hat{SE} = 0.06$ ; Nichols et al. 1992) are similar to our estimates. Because our estimates of apparent survival are generally lower than those observed for other swan populations, and because productivity of Izembek swans is lower and more variable than observed for swans elsewhere in Alaska (Meixell 2007), we suggest that the Izembek population may be unable to sustain a constant population size through reproduction alone.

## **Inference from a Marked Sample**

Estimates of demographic parameters contingent on a sample of individuals are subject to true biological variation (process variance) in addition to variation resulting from sampling (sampling variance; Burnham et al. 1987). Sampling variances associated with estimates of survival rates are dependent upon several factors (e.g., sample sizes of marked individuals) that are independent of true variation in survival (Gould and Nichols 1998). As a result, our estimated variation in apparent survival may be positively biased in respect to true variation in survival. However, our estimates of process variation for adult ( $\sigma = 0.19$ ) and immature ( $\sigma = 0.21$ ) swans indicate that a large proportion of the total variation (ASY = 0.21, immature = 0.25) in survival among years was a result of true biological variation. We acknowledge that our estimates of process variation are relatively imprecise, but even at the lower bound of the estimate (ASY = 0.13, immature = 0.14), more than half of the observed variation in survival is estimated to be true biological variation.

Several studies reported reduced survival probabilities for neck-collared geese (e.g., Schmutz and Morse 2000, Alisauskas and Lindberg 2002), and Meixell (2007) observed a lower survival probability to fledging for neck-collared cygnets. Collars may induce mortality as a result of icing or increased energetic demand (Alisauskas et al. 2006). If neck-collaring influences survival probability, survival estimates based on the marked sample are negatively biased (Pollock et al. 1990). Additionally, heterogeneity in mortality risks associated with neck collars across populations, as a result of variation in wintering areas (e.g., possibility of collar icing), would obscure the comparison of

results. The effect of collars on survival of post-fledging swans has not been investigated; however, estimates of apparent survival from collared swans across several migratory and non-migratory populations are relatively high and consistent (Bart et al. 1991b). Therefore, although survival rates may be reduced by the presence of collars, we suggest that collars were not a primary factor responsible for our low and variable estimates of apparent survival.

Failure to account for collar loss results in negatively biased estimates of apparent survival (Arnason and Mills 1981, Nichols and Hines 1993). Our results indicate that collars were lost at high rates when applied to ASY males, but at a considerably lesser extent for other age and sex classes. This is consistent with the findings of other studies of tundra swans (Allen et al. 1991, Nichols et al. 1992), and sex-specific differences in collar retention are also well documented for geese (e.g., Johnson et al. 1995, Wiebe et al. 2000). Higher rates of collar loss in male geese have been attributed to their larger size and aggressive behavior (Samuel et al. 1990). It is likely that the same mechanisms affect collar retention in swans. The thicker collar type (TYPE II), applied during the last 8 years of our study, substantially reduced the rates of collar loss for ASY males and almost eliminated collar loss for other age and sex classes. Nichols et al. (2002) found evidence supporting a correlation between collar retention rates and time since banding. We did not assess this factor; however at least 13 of 20 losses were known to occur in the first 2 years after banding. Although it is likely that the plastic deteriorates over time (Samuel et al. 2001), it appears that for our population, collar loss was more a function of age of the marked individual and their sex rather than time since application of the collar

and may be related to poorly sized or glued collars (Samuel et al. 2001) combined with individual heterogeneity in tolerance of collars.

### **Implications for the Izembek Population**

Our estimates of apparent survival combined with low and variable estimates of productivity (Meixell 2007) indicate that immigration into the Izembek breeding grounds is necessary to sustain a local tundra swan population. However, unique non-migratory behavior and potential morphometric differences (C. P. Dau, U.S. Fish and Wildlife Service and J. M. Pearce, U.S. Geological Survey, unpublished data) suggest that the Izembek population may be functionally isolated from other WP swans. These observations would seem to be in conflict as functional isolation cannot exist if immigration is occurring. We further consider the implications of our results relative to 2 competing hypotheses: 1) the Izembek population is functionally isolated from other WP swans, and 2) the Izembek population is open to immigration from other breeding areas.

*Isolated Population.* Swans neck-collared on the Pavlof units of the Alaska Peninsula National Wildlife Refuge, the nearest tundra swan habitat to the northeast of our study area, are thought to be entirely migratory and were never observed intermixed with Izembek swans on breeding grounds or Unimak Island wintering grounds (Dau and Sarvis 2002). Thus, if immigration were occurring, the Pavlof population would be a logical source of immigrants, yet such movements were never observed. We lack resight data in Alaska during the 3-year period in which population abundance increased by 68% (1988–1991). Thus, if marked individuals dispersed at temporally varying rates during

the years of our analysis, but returned to the study area during the 3-year period immediately following our analysis (1988–1991), they would have been interpreted as losses to the population by our models. As a result, our estimates of apparent survival may be negatively biased such that true survival of Izembek swans is of sufficient magnitude to account for low rates of productivity. Therefore, tundra swans associated with the Izembek breeding grounds may represent an isolated subpopulation that is supported primarily through within-population reproduction.

*Open Population.* Our regression analysis predicted a negative linear trend in population abundance (1980–2006), yet on 2 occasions, abundance was bolstered by large increases occurring within a 4-year time period (1988–1991 = 68% increase; 2002–2006 = 302% increase). These dramatic increases in abundance are not feasible given estimates of productivity (Meixell 2007) and therefore would seem to indicate the occurrence of immigration into the Izembek breeding grounds (Dau and Sarvis 2002). Our low and variable estimates of apparent survival indicate that permanent emigration is an important source of loss to the Izembek population. Given high rates of nest failure (Meixell 2007) and likely high rates of dispersal, the number of years swans remain associated with our study area may be related to rates of productivity (Johnson et al. 1992, Haas 1998) such that those experiencing unfavorable reproductive success disperse, while those experiencing high reproductive success remain. Therefore, although reproduction by Izembek swans likely contributes to recruitment of individuals to the population, the Izembek breeding grounds may represent a population sink with

sub-optimal breeding habitat (Pulliam 1988) whereby long-term maintenance of population abundance is influenced primarily by immigration from elsewhere. Future studies designed to directly examine the degree of genetic isolation of Izembek swans are needed to distinguish between these 2 hypotheses.

## **MANAGEMENT IMPLICATIONS**

Apparent survival probability was lower for tundra swans associated with the Izembek population than for other North American swan populations. We attribute low and variable rates of apparent survival to high and variable rates of permanent emigration and suggest that combined estimates of apparent survival and reproductive success for the Izembek population are of insufficient magnitude to maintain a stable population. Therefore, immigration into the Izembek breeding grounds may be necessary to sustain a breeding population. However, some evidence exists suggesting that the Izembek population is isolated from other breeding areas, and is therefore sustained primarily through reproduction. We lack the ability to thoroughly assess the degree of genetic isolation in the Izembek population, and therefore recommend that future research focus on genetic and morphometric analysis of swans on the Izembek breeding grounds relative to other breeding areas. Variation in abundance of small local populations is sensitive to environmental and demographic stochasticity, and therefore these populations are at greater risk of extinction (Lande et al. 2003). As a result, management efforts to increase productivity of Izembek swans may positively influence population growth (Koons et al.

2006), consequently reduce breeding dispersal, and ultimately act to limit annual variation in abundance and contribute to the longevity of an Izembek breeding population.

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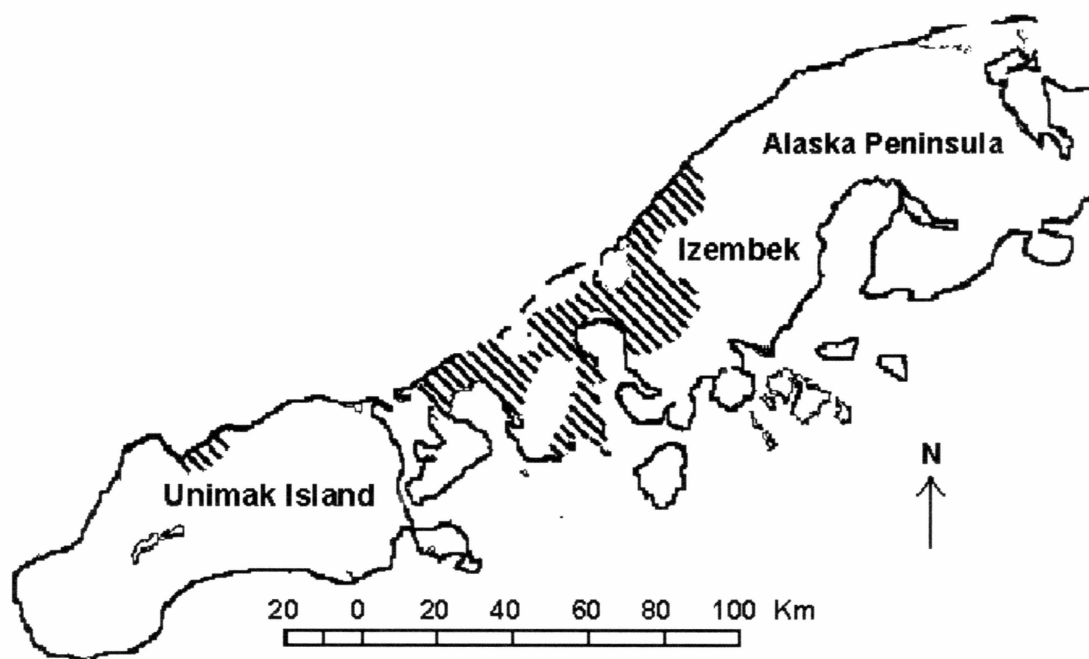


Figure 1. Location of study site on and adjacent to Izembek National Wildlife Refuge, Alaska Peninsula, USA. Shaded regions represent sampling areas on the Izembek breeding grounds and Unimak Island wintering grounds.

Interval type:	( 1 <sup>st</sup> Closed ) ( 1 <sup>st</sup> Open ) ( 2 <sup>nd</sup> Closed ) ( 2 <sup>nd</sup> Open )			
Encounter type:	Captures and Resightings	Resightings and Recoveries		
Parameters estimated:	$p_i$	$\varphi_i, R_i, R'_i, \lambda_i$		$\psi_i$
Constraints:		$\psi_i = 0$	$p_i = 0$	$\varphi_i = R_i = R'_i = \lambda_i = 1$
	17 July	16 July	2 September	

Figure 2. Illustration of sampling and modeling intervals for demographic analysis of tundra swans neck-collared on and adjacent to Izembek National Wildlife Refuge on the lower Alaska Peninsula, USA. The second closed and open intervals were added for modeling purposes, estimates of  $\varphi$  correspond to the first open interval, and state transition (collar loss) is assumed to occur immediately prior to closed sampling intervals.

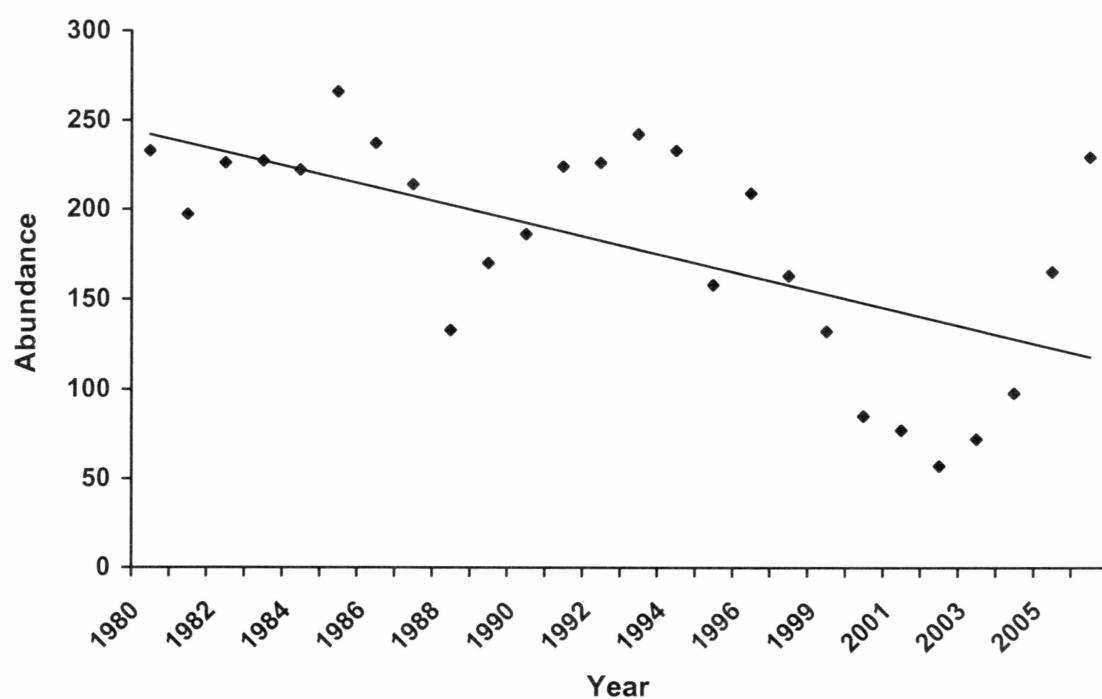


Figure 3. Abundance of tundra swans on and adjacent to Izembek National Wildlife Refuge, Alaska Peninsula, USA. Surveys were conducted annually during 1980–2006 (excluding 1997) in late May to early June.  $\text{Abundance} = 9782.82 + -4.82 * \text{year}$ ,  $R^2 = 0.38$ ,  $p < 0.05$ ,  $df = 25$ .



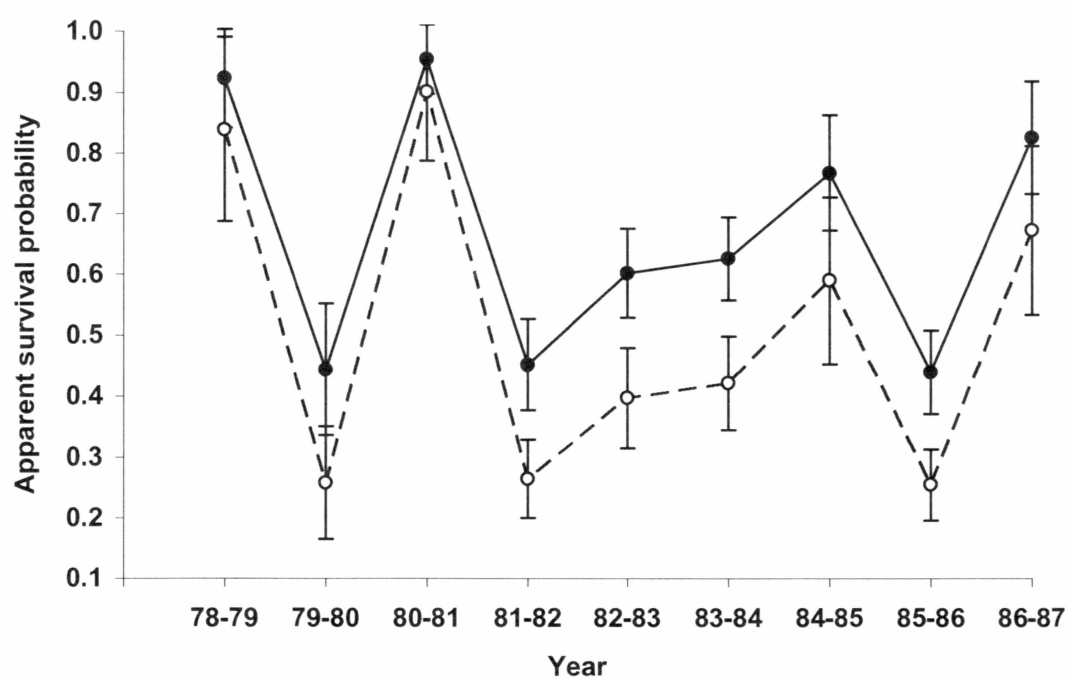


Figure 4. Estimates of annual, apparent survival probability ( $\hat{\phi} \pm 1 \text{ SE}$ ) of neck-collared tundra swans on the lower Alaska Peninsula, USA, 1978–1989. Dark circles depict estimates for adults (after-second-year); light circles depict estimates for immatures (hatch-year and second-year). The age effect is additive.

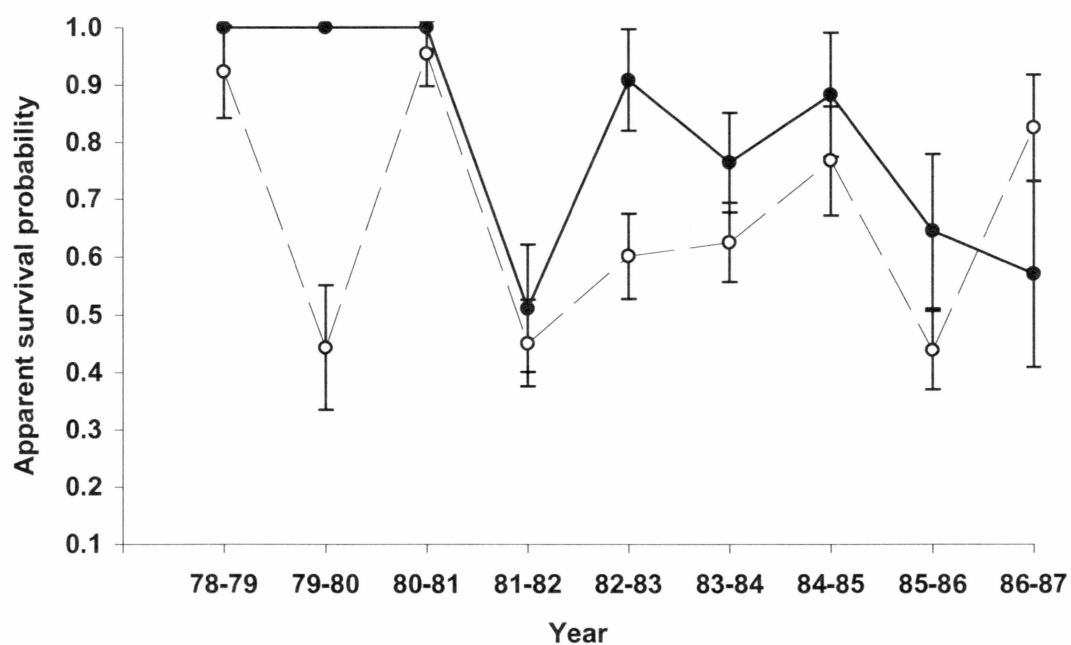


Figure 5. Estimates of annual, apparent survival probability ( $\hat{\phi} \pm 1 \hat{SE}$ ) of neck-collared tundra swans on the lower Alaska Peninsula, USA, 1978–1989. Dark circles depict estimates for swans known to breed on and adjacent to Izembek National Wildlife Refuge; light circles depict estimates for all marked adult (after-second-year) swans.

Table 1. Summary of the number of releases, recaptures, resightings, and recoveries of tundra swans neck-collared on the lower Alaska Peninsula, USA, 1978–1988. Releases and recaptures occurred during closed intervals, 18 July–3 September, while resightings and recoveries occurred during open intervals between 2 September of the year listed and 17 July of the following year.

Observation type	Age	Year											Total
		78	79	80	81	82	83	84	85	86	87	88	
Releases <sup>a</sup>	HY <sup>c</sup>	8	0	8	17	13	39	8	18	13	24	6	154
	SY <sup>d</sup>	3	6	9	12	4	3	2	23	1	28	18	109
	ASY <sup>e</sup>	16	11	26	41	38	39	5	19	4	38	18	255
Recaptures	HY	-	0	1	0	2	5	1	6	0	8	1	24
	SY	-	0	3	1	5	2	1	0	0	0	0	12
	ASY	-	4	3	12	10	9	10	7	7	10	5	77
Resightings <sup>b</sup>	HY	6	2	5	13	12	23	7	12	14	12	1	107
	SY	3	5	8	13	6	7	3	12	2	6	7	72
	ASY	12	13	28	43	35	43	19	25	16	16	9	259
Recoveries	HY	0	0	0	0	0	0	1	0	0	5	1	7
	SY	0	0	0	1	0	0	0	0	0	1	2	4
	ASY	0	0	0	0	0	0	0	1	0	0	1	2

Table 1 continued.

<sup>a</sup> Number of swans fitted with original or replacement neck collars.

<sup>b</sup> The number of resightings listed is the number of individuals observed at least once within the given interval conditional on not being recovered.

<sup>c</sup> HY = hatch-year

<sup>d</sup> SY = second-year

<sup>e</sup> ASY = after-second-year

Table 2. Number of previously neck-collared swans captured without collars, on the lower Alaska Peninsula, USA, 1978–1988. Occurrences are grouped by collar type, swan age at time of banding, and sex.

Collar type	Age and sex <sup>c</sup>	Years since initial release					Total
		1	2	3	4	5	
TYPE I <sup>a</sup>	SY M <sup>d</sup>	1	1	0	0	0	2
	ASY M <sup>e</sup>	1	3	1	2	0	7
	ASY F <sup>f</sup>	0	1	0	0	0	1
TYPE II <sup>b</sup>	ASY M	2	2	0	2	1	7
	HY M <sup>g</sup>	1	0	0	0	0	1
	ASY F	1	0	1	0	0	2

<sup>a</sup> Thinner collar type applied to swans during 1978–1980.

<sup>b</sup> Thicker collar type applied to swans during 1981–1988.

<sup>c</sup> Only includes age classes for which collar loss was documented.

<sup>d</sup> SY M = second-year males.

<sup>e</sup> ASY M = after-second-year males.

<sup>f</sup> ASY F = after-second-year females.

<sup>g</sup> HY M = hatch-year males.

Table 3. Models of annual, apparent survival ( $\phi$ ) and detection probability ( $p$ ) for neck-collared tundra swans on the lower Alaska Peninsula, USA, 1978-1989. Models are ranked by Akaike's Information Criterion differences ( $\Delta\text{AIC}$ ). We included only models with AIC model weight  $> 0.00$ .

Model <sup>a</sup>	K <sup>b</sup>	$\Delta\text{AIC}$	Log $L$	$w_i^c$
$\phi$ (year + age2) $p$ (age3)	21	0	-1132.48	0.66
$\phi$ (year + age3) $p$ (age3)	22	1.66	-1132.31	0.29
$\phi$ (year + age2) $p$ (.)	19	7.67	-1138.32	0.01
$\phi$ (year + age2) $p$ (year)	27	7.79	-1130.38	0.01
$\phi$ (year + age3) $p$ (year)	28	8.68	-1129.83	0.01
$\phi$ (year + age3) $p$ (.)	20	8.70	-1137.83	0.01

<sup>a</sup> All models contained additional fixed parameters:  $\psi$ ,  $\lambda$ ,  $R$ , and  $R'$ . Abbreviations: age2 = immature (hatch-year, second-year) and after-second-year; age3 = hatch-year, second-year, and after-second-year.

<sup>b</sup> Number of parameters.

<sup>c</sup> AIC model weight

Table 4. Models of annual, apparent survival ( $\varphi$ ) of neck-collared tundra swans known to breed on the lower Alaska Peninsula, USA, 1978-1989. Models are ranked by Akaike's Information Criterion differences ( $\Delta\text{AIC}$ ).

Model <sup>a</sup>	K <sup>b</sup>	$\Delta\text{AIC}$	$\text{Log } L$	$w_i^c$
$\varphi(\text{year})$	7	0	-327.40	1.00
$\varphi(.)$	1	17.33	-342.07	0.00
$\varphi(\text{sex})$	2	19.25	-342.03	0.00

<sup>a</sup> All models contained additional fixed parameters:  $p$ ,  $\psi$ ,  $\lambda$ ,  $R$ , and  $R'$ .

<sup>b</sup> Number of parameters.

<sup>c</sup> AIC model weight.

## CONCLUSIONS

I conducted a detailed demographic analysis of long-term (1978–1996) tundra swan data collected on and adjacent to Izembek National Wildlife Refuge (NWR) on the lower Alaska Peninsula. I estimated several individual demographic parameters and assessed their relationship relative to a number of environmental and ecological factors. My results indicate that rates of productivity (1980–96; Chapter 1) and adult apparent survival (1978–1986; Chapter 2) of Izembek tundra swans were lower and more variable than observed for other species and populations of swans throughout their range.

Contrary to expected trends of increasing productivity with distance south of the Arctic as a result of longer breeding seasons in southern latitudes (Wilk 1988, Monda et al. 1994, Babcock et al. 2002), my results indicate that levels of productivity were low and variable over much of the study area. Predation has been identified as the primary source of mortality during the breeding season for North American waterfowl (Sargeant and Raveling 1992), although given the large size and aggressive behavior of incubating tundra swans, few predators are capable of depredating swans nests (Hawkins 1986). However, previous studies of nesting swans have identified brown bears as a threat to reproductive success (Monda et al. 1994), and densities of brown bears on the Izembek breeding grounds are among the highest of any tundra swan breeding areas (Miller et al. 1997). I suspect that nest depredation by bears was the primary source of nest failure to Izembek swans, and my results indicated considerable differential success between high and low bear density areas. Therefore, I suggest that predation by brown bears was a primary determinant of tundra swan reproductive success. Furthermore, I suggest that



nest depredation by bears in remote portions of the study area was of sufficient magnitude to negate the positive effects of long breeding seasons (Wilk 1988), and in fact, result in productivity levels that were lower than in northern latitudes. I recommend that the goals and objectives of bear management on and adjacent to Izembek NWR take into consideration the effects of bear density on tundra swan population dynamics.

My estimates of annual, apparent survival probability for neck-collared adult swans are among the lowest reported for swan survival across species and populations (Bart et al. 1991). For long-lived waterfowl species such as swans and geese, adult survival rates in stable populations are expected to be relatively high and invariable to account for relatively low levels of reproductive output (Charlesworth 1994). Estimates of apparent survival may be lower than true survival as a result of confounding between permanent emigration and mortality (Lindberg et al. 2001); however, reductions in apparent survival represent losses to a population, and therefore represent the probability that individuals remain associated with the study area. I suspect that emigration was a primary source of losses to the Izembek population and attribute notably low estimates in several years to high rates of emigration.

Given existing data, I am unable to thoroughly assess the degree to which the Izembek population is isolated from other breeding populations and therefore present 2 hypotheses relative to the interpretations of my results and implications for the Izembek population: 1) the Izembek population is functionally isolated from other WP swans and is supported primarily through within-population reproduction, and 2) the Izembek breeding grounds represent a population sink (Pulliam 1988) in which long term

population abundance is supported primarily through immigration by swans from elsewhere. If the Izembek population is functionally isolated, I suspect that long-term temporary emigration by marked individuals resulted in negatively biased estimates of apparent survival such that true survival of Izembek swans is higher than predicted by my models. Alternatively, if immigration is important for sustaining an Izembek breeding population, then I suggest that permanent emigration is a primary source of losses to the population and, furthermore, may be influenced by reproductive success (Johnson et al. 1992, Haas 1998).

Local populations that are small and exhibit a large degree of annual variation in abundance are of particular concern because they have an increased risk of extinction (Lande et al. 2003). Management actions that increase levels of productivity, even among long-lived species, are expected to positively influence short-term population growth rates, and may lead to desirable increases in long-term abundance (Koons et al. 2006). Furthermore, because rates of breeding dispersal are likely influenced by reproductive success in previous nesting attempts (Johnson et al. 1992), management to increase productivity of Izembek swans may also act to reduce rates of breeding dispersal, and therefore facilitate moderation of fluctuations in population abundance.

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